A sequential Bayesian methodology to estimate movement and exploitation rates using electronic and conventional tag data: application to Atlantic bluefin tuna (*Thunnus thynnus*)

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Abstract: This paper presents a Bayesian methodology to estimate fishing mortality rates and transoceanic migration rates of highly migratory pelagic fishes that integrates multiple sources of tagging data and auxiliary information from prior knowledge. Exploitation rates and movement rates for Atlantic bluefin tuna (*Thunnus thynnus*) are estimated by fitting a spatially structured model to three types of data obtained from pop-up satellite, archival, and conventional tags for the period 1990–2006 in the western North Atlantic. A sequential Bayesian statistical approach is applied in which the key components of the model are separated and fitted sequentially to data sets pertinent to each component with the posterior probability density function (pdf) of parameters from one analysis serving as the prior pdf for the next. The approach sequentially updates the estimates of age-specific fishing mortality rates (F) and transoceanic movement rates (T). Estimates of recent F are higher than the estimated rate of natural mortality and higher in the east than in the west. Estimates of annual T from the west to the east are higher for larger fish (6% for ages 0–3 to 16% for ages 9+). These estimates are also higher than those obtained from tagging studies before the 1990s and could be associated with changes in stock composition.

Résumé : Notre travail présente une méthode bayésienne pour estimer les taux de mortalité dus à la pêche et les taux de migration transocéanique de poissons pélagiques fortement migrateurs qui intègre de multiples sources de données de marquage et des informations auxiliaires provenant de connaissances antérieures. Nous estimons les taux d'exploitation et de déplacement des thons rouges (*Thunnus thynnus*) en ajustant un modèle à structure spatiale à trois types de données provenant d'étiquettes satellites détachables, d'étiquettes enregistreuses et d'étiquettes ordinaires durant la période 1990–2006 dans l'ouest de l'Atlantique Nord. Nous utilisons une approche statistique bayésienne séquentielle dans laquelle les composantes essentielles du modèle sont séparées et ajustées séquentiellement à des ensembles de données pertinentes à chaque composante et dans laquelle la fonction de densité de probabilité (pdf) a posteriori des paramètres d'une analyse servent de pdf a priori pour l'analyse suivante. Cette approche remet à jour séquentiellement les estimations des taux de mortalité dus à la pêche en fonction de l'âge (F) et les taux de déplacements trans-océaniques (T). Les estimations des F récents sont supérieures aux taux estimés de mortalité naturelle et plus élevées dans l'est que dans l'ouest. Les estimations du T annuel de l'ouest vers l'est sont supérieures pour les poissons plus grands (6 % aux âges 0–3 à 16 % aux âges 9+). Ces estimations sont aussi supérieures à celles faites à partir des études de marquage antérieures aux années 1990 et pourraient être reliées à des changements de composition de stocks.

[Traduit par la Rédaction]

Introduction

Mark–recapture data sets enable estimation of movement and exploitation rates if tagged fish are representative of the target population, if all recaptured tags are reported or the reporting rate is known, and if the behavior of the fish is not impacted by tagging (Pollock 1991; Sibert et al. 1999; Pine et al. 2003). Uniquely identified conventional tags have long been used in fisheries to investigate mortality rates, population size, growth rates, and movement (Quinn and Deriso 1999; Walters and Martell 2004). More recently, electronic tags, which provide detailed and continuous infor-

Received 18 December 2007. Accepted 10 September 2008. Published on the NRC Research Press Web site at cjfas.nrc.ca on 12 February 2009.
J20326

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mation such as light level, location, pressure, and temperature data, have been developed and applied mainly to highly migratory species such as tunas (Block et al. 1998, 2001, 2005). Pop-up satellite archival tags (or "pop-up satellite tags") are a unique fisheries-independent tag developed specifically to examine movements without the bias of fisheries interactions. Subject to a limit on information transfer due to bandwidth and battery capacity, the tags summarize archived data and transmit information to a satellite. To date, most tracks on bluefin tuna range from 1 to 9 months. In contrast, implanted archival tags (or "archival tags") offer the advantage of long-term retention and retrieval of a higher-resolution time series for up to several years. Both of these electronic tags have been used extensively to investigate fish movement patterns, behavioral ecology, and thermal biology (Weng et al. 2005; Wilson et al. 2005; Schaefer et al. 2007). Compared with conventional tagging experiments, the number of electronic tags released in a program is often limited because deployment and recapture of these tags are expensive. Electronic tag data, however, can be used to estimate mortality rates because they have an advantage over conventional tags in that reporting rates are expected to be higher due to higher tag-return rewards and enhanced publicity. To date, however, there has been very little research seeking to estimate exploitation rates from electronic tag data.

Bluefin tuna are one of the most economically valuable fish in the world, with prices reaching US$1000/kg in the Tokyo Tsukiji market. Because of its declining stock status, research on and fisheries management of Atlantic bluefin tuna (*Thunnus thynnus*) in the North Atlantic Ocean have received a great deal of attention (ICCAT (International Commission for the Conservation of Atlantic Tunas) 2007; Kell and Fromentin 2007), including an extensive electronic tagging campaign (Block et al. 2005; Wilson et al. 2005). ICCAT regulates the fishery by setting annual quotas for each member country in each of two management zones (separated by the 45°W meridian): (*i*) the Western Atlantic and (*ii*) the Eastern Atlantic and Mediterranean Sea. In the western Atlantic, the main fishing fleets are rod-and-reel, longline, and purse seine, and in the east, there are a variety of fleets such as purse seine, bait boat, trap, and longline. There have, however, been controversies regarding the population structure and the current level of transoceanic migrations. Conventional tag programs conducted for small fish (mainly ages 1–3) by USA since 1954 (Mather et al. 1995) have indicated low trans-Atlantic migration rates from west to east (about 1%; National Research Council (NRC) 1994). In contrast, archival and pop-up satellite tag research, which targeted larger fish released in the western Atlantic (mainly ages 7–10), showed higher occurrence of transoceanic migrations (Block et al. 2001, 2005). Additionally, these researchers identified that there are at least two population components involved in trans-Atlantic movements, which have different spawning grounds (the Gulf of Mexico and the Mediterranean Sea), further complicating estimations owing to mixing on foraging grounds.

In recent ICCAT stock assessments, an ADAPT virtual population analysis (VPA) model (ICCAT 2007) has been used to provide management advice. Although this is applied to fisheries catch-at-age data and various abundance indices, it does not incorporate tagging information and currently ignores any mixing of stocks. Migration rates are key factors in estimating exploitation rates in metapopulation situations (Walters and Martell 2004). They can also influence the defining of the boundaries in management zones. Therefore, for better stock management, it is essential to develop new models of fishing mortality and the transoceanic migration rates using all sources of tagging data.

Bayesian state–space models are among the most powerful tools for fishery stock assessments when available data and information are sparse (Meyer and Millar 1999; Rivot et al. 2004). They offer a statistically rigorous approach to account for and reduce uncertainties by providing a probabilistic framework and incorporating both process and observation (measurement) errors. Recently, quantitative stock assessment models with many parameters have been developed to integrate multiple data sources (e.g., Hampton and Fournier 2001; Maunder and Watters 2003). It is common for a single model to be fitted to all available data sets at one time for parameter estimation. This, however, may complicate reaching and identifying numerical convergence and introduce computational burden, owing to the estimation of many parameters, although there are some techniques to diminish these problems (e.g., some of the parameters can be fixed initially to get reasonable starting values for the other parameters). To overcome the challenges of combining multiple data sources and auxiliary information, a sequential Bayesian approach (Gelman et al. 2004) has been proposed and applied in stock assessments (Myers and Mertz 1998; Michielsens et al. 2008). In the sequential approach, different data sets can be analyzed separately with models specialized for each data set. By using posterior distributions of parameters of interest as prior probability density functions (pdfs) in subsequent analyses, multiple data sets and auxiliary information can be integrated efficiently and reliably.

In this paper, a state–space tagging model (e.g., Mäntyniemi and Romakkaniemi 2002; Michielsens et al. 2006) that follows a sequential Bayesian estimation approach is presented and illustrated with an application to Atlantic bluefin tuna. Exploitation rates and transoceanic movement rates from 1990 to 2006 are estimated from two types of electronic tags, pop-up satellite tags and archival tags, as well as from conventional tag data sets. These three types of tags have different characteristics in terms of information provided on movements and mortality by age. In addition, they each provide information on the fisheries dependence in tag recapture. The statistical analyses of these data provide estimates of area- and age-based fishing mortality rates that account for movement rates by age.

Materials and methods

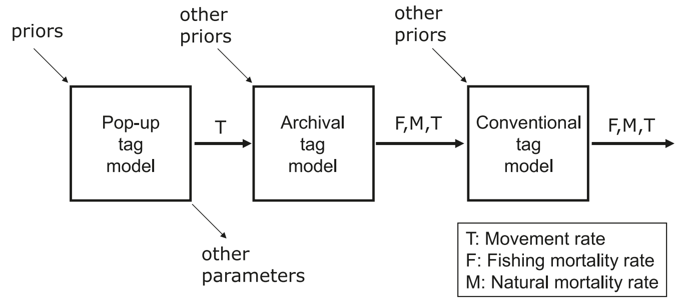
A spatially and age-structured model is formulated that tracks the fate of each tagged group defined by tag type, release year, release area, and age. A Bayesian state–space estimation approach is applied that treats all estimated parameters as random variables and requires a prior pdf (or "prior") to be assigned to the estimated variables. It estimates fishing mortality rate, F, in each area by age group, tag reporting rates by tag type, and annual crossover rates by age group. The rate of natural mortality, M, is also treated as a random variable but with high prior precision. In the state–space modeling framework, both observation error and process error are explicitly modeled.

The empirical basis for parameter estimation derives from the comparison of model predictions with observations of the number of tags of a given tag type recaptured in a given area. Pop-up satellite, archival, and conventional tags are modeled separately, and different assumptions are made about the information contained in each tag type and about tag fate. For example, the key process modeled for pop-up satellite tags is movement. In contrast, for internally implanted archival tags and externally placed conventional tags, the recapture observation is treated as a reported fishing mortality event. Further structural assumptions are made about tag reporting rates. It is assumed that tag reporting rates are higher for archival tags than for conventional tags primarily due to the enhanced reward structure that provides US$1000 for archival tags versus a hat for conventional tags.

A sequential Bayesian approach (Michielsens et al. 2008) is formulated to integrate information from the three kinds of tags. This approach consists of three parts in the current study (Fig. 1). First, the posterior pdfs of movement rates are estimated from pop-up satellite tag data along with other nuisance parameters. Next, the posterior pdf of movement rates is used as the prior pdf of these parameters for archival tag modeling, which in turn will provide posteriors of movement rates and fishing mortality rates. These estimates are for after 1997, when the archival tag data started to accumulate. Finally, the posterior from the archival tag modeling is used as the prior for conventional tag modeling. The distributions of estimates including fishing mortality rates between 1990 and 1996 are updated by conventional tag information. The sequential order of the analysis of the three kinds of tags was determined according to model input requirements and to most readily facilitate numerical convergence of the Markov chains. The pop-up satellite tag model was simplest and had the fewest input requirements and was thus analyzed first. The archival tag model was intermediate in complexity and could utilize the key posterior outputs of the pop-up satellite tag model as priors. The conventional tag reporting rates were conditional on values for reporting rates of archival tags, and it was thus necessary to run the archival tag model before the conventional tag model. If suitable priors could be formulated, however, parameters could be estimated simultaneously in a single model without applying the sequential approach. The archival and conventional tag data sets may be good candidates for this alternative approach because the model structure applied to them is almost same.

We have selected 1990 as the starting year because the model applied assumes consistency of fishing patterns and tagging activities in its estimation of parameters, and fishing operation patterns are considered to have changed with rapidly increasing catches after 1990. Conventional tagging on Atlantic bluefin tuna in the Western Atlantic started in the 1950s and was conducted actively in the 1960s–1970s and 1990s. However, there were few tag releases in the 1980s, which provides another reason for setting the starting year as 1990. Many of the tags in the 1990s were released in a common set of experiments in which fish were tagged with conventional, archival, or satellite tags in the winter fishery off North Carolina.

Fig. 1. Framework of the Bayesian sequential approach that was applied in the analysis of pop-up satellite, archival, and conventional tagging data for Atlantic bluefin tuna (*Thunnus thynnus*).



Data

Release and end point data of the three kinds of tags are used for modeling. The full track data available from the application of geolocation algorithms used to estimate a track from archival and pop-up satellite tags are not used in this current analysis, despite being of high value for understanding fine-scale detail in migration patterns. We envision a two-step approach for the incorporation of tag data sets that contain migration patterns. We regard this paper as the first step in a longer-termed, multistage research effort to develop mathematical approaches for modeling these novel types of tagging data. The release and endpoint location for pop-up reporting to satellite or fisheries recapture are categorized into two spatial areas (west and east) in the North Atlantic Ocean separated by the 45th degree W meridian. We use the same definition as the ICCAT geographical delimitation, because it is necessary to examine the validity of this zone definition and evaluate the low migration rate hypothesis.

Pop-up satellite tag

Pop-up satellite tags were attached to Atlantic bluefin tuna (ages 4–16, mainly 7–10) using monofilament leaders and titanium darts (Block et al. 2001, 2005). These tags record information on light levels, ambient water temperature, and pressure and, to date, are attached to bluefin tuna for less than a year. The tags detach on a user-defined date, or when prematurely released, and transmit archived data to Argos satellites. The Argos satellite system calculates the pop-up endpoint locations of the tags using the Doppler shift of the radio transmissions (Taillade 1992). In the current generations of pop-up satellite tags, the tag will detach from the fish if the animal goes below a preset depth or remains at a constant depth (e.g., as if on the bottom or at the surface for a user-set number of hours), which often is indicative of fish mortality or premature detachment of the tag. We examined 320 records from pop-up satellite tags deployed on Atlantic bluefin tuna that successfully popped up from 1997 to 2006 in 22 independent tagging campaigns by the TAG-A-GIANT program of the Tuna Research and Conservation Center (TRCC) (Table 1). In this set of deployments, 296 pop-up satellite tags were deployed in the western Atlantic management unit and 24 were deployed in the eastern Atlantic. The results were compiled to represent

Table 1. The number of tag releases and return rates (%; number of reported recaptures / number of releases) by age groups (ages 0–3, 4–8, and 9+) for three tags used for this analysis.

	Pop-up tag				Archival tag				Conventional tag					
	No. releases		Return rate		No. releases		Return rate		No. releases			Return rate		
	4–8	9+	4–8	9+	4–8	9+	4–8	9+	0–3	4–8	9+	0–3	4–8	9+
1990									212	97	2	6.6	6.2	0.0
1991									733	59	7	4.1	1.7	0.0
1992									754	59	2	4.1	8.5	0.0
1993									434	101	7	5.8	5.9	0.0
1994									88	141	69	6.8	9.9	10.1
1995									640	315	309	8.4	6.0	7.1
1996									246	933	197	1.6	6.5	2.5
1997	35	1	91.4	100.0	153	5	26.8	0.0	650	1148	125	4.9	6.3	7.2
1998	0	8		75.0					1433	89	48	3.9	0.0	6.3
1999	1	3	100.0	0.0	73	36	30.1	33.3	327	210	19	2.1	0.5	5.3
2000	32	21	71.9	52.4					148	307	5	2.7	1.3	0.0
2001	47	37	68.1	78.4					151	132	15	0.7	1.5	0.0
2002	49	14	89.8	92.9	17	1	17.6	0.0	340	135	16	2.1	1.5	12.5
2003	12	9	100.0	88.9	99	8	16.2	12.5	239	17	24	0.8	5.9	0.0
2004	0	19		89.5	50	43	4.0	9.3	1404	14	32	0.4	0.0	0.0
2005	2	26	100.0	84.6	45	20	2.2	0.0	152	9	27	0.0	0.0	0.0
2006	1	3	100.0	66.7	2	3	0.0	0.0	79	10	5	2.5	0.0	0.0

the numbers of tags that had popped off in each of the two spatial areas.

Archival tag

Archival tags were surgically implanted into the peritoneal cavity of the fish (Block et al. 2001, 2005). The archival tags deployed measured light intensity, depth, ambient seawater temperature, and peritoneal temperatures for up to 5 years. The tags require recapture to recover the time series data set. The endpoint locations of the tags were reported by the fishers recapturing the fish. In this analysis, 556 archival tags deployments from 11 tagging experiments conducted by the TAG-A-GIANT program were compiled (Table 1). All tags available for the analysis were released in the western Atlantic management area. All 101 recapture records (data up until 2006) have information on recapture locations and dates. The age range of the fish with archival tags is from 4 to 13 years of age (primarily from 7 to 10).

Conventional tag

We examined conventional tag data recently made available by the US National Marine Fisheries Service (NMFS). Data from other Atlantic bluefin tuna tagging activities (releases from the eastern Atlantic Ocean) were not used. The ICCAT tagging database includes a number of conventional tags released mainly from Spain in the early 1990s. The tag return rate (total number recaptured and reported / number released), however, was very low and most of the recaptures occurred within one year in Spain. Therefore we suspected that this tagging program might not reflect the eastern area as a whole and we refrained from incorporating the data released in the east into the current model. The NMFS database included 45 223 release records since 1954. In this analysis, 12 715 tags that were released after 1990 and had exact records of date, location, and fish length at release were analyzed (Table 1). We checked the database to remove duplicates or ambiguities. Return rates in the late 1960s were about 30% but declined to <10% in the 1990s. In particular, return rates after 1999 were very low (less than 5%). This could be interpreted as a decrease in fishing mortality and (or) reporting rate (for other possibilities, see Discussion). The majority of conventional tags were attached to juvenile fish of ages 1–2. In recent years, in conjunction with the TAG-A-GIANT program, as well as the winter Carolina fishery resurgence in the mid-1990s, several thousand conventional tags were deployed on larger fish of ages 4+.

For all three tag types, the age of tagged and recaptured fish was estimated based on measured length at deployment. The age–length growth models of Turner and Restrepo (1994) and Cort (1991) were used to estimate the age of fish released in the west and east, respectively. In this analysis, the uncertainty of the age determination was not considered. As explained later, the present model estimates fishing mortality and movement rates for three age categories, instead of each age. Thus, the effect of any uncertainty in age estimation on the final estimates was considered to be small.

Population dynamics

Basic structure

This age-structured model included two spatial areas and had an annual time step for archival and conventional tags and quarterly time steps for pop-up satellite tags. All satellite tag records had a reporting pop-up date within a year of release. All fleets in each area were aggregated, ignoring any differences in reporting rates and harvest rates between fleet types. It was presumed that movement occurred earlier in each time step, and afterwards, natural mortality and fishing mortality were experienced by the fish. This model does not account for genetic stock structures, and all fish are

Table 2. Lists of indices, model variables, data, and model parameters used for this analysis.

Symbol	Description
Indices	
c	Tag type (1, pop-up satellite tag; 2, archival tag; 3, conventional tag)
Y	Release year
a	Fish age or age group (1, ages 0–3; 2, ages 4–8; 3, ages 9+)
A	Release area (1, west of the 45°W meridian; 2, east of 45°W meridian)
i, j	Area
t	Time step (year) or time period (years)
b	Quarter programmed for pop-up tags to release
d	Quarter at liberty of tagged fish within a year (1, 0–3 months; 2, 4–6 months; 3, 7–9 months; 4, 10–12 months)
Model variables	
$N_{c,Y,a,A,i,t}$	Expected number of fish carrying tag type c, released in year Y, of age a, released in area A, residing in area i at the beginning of time t
$N^{*}_{c,Y,a,A,i,t}$	Expected number of fish carrying tag type c, released in year Y, of age a, released in area A, residing in area i after fish movement in time t
$C^{p}_{1,Y,a,A,i,b,d}$	Expected number of pop-up tags that successfully transmit stored data that were released in year Y, in area A, reside in area i, after d quarters that were programmed to release in the bth quarter at liberty
$C^{p}_{c,Y,a,A,i,t}$	Expected number of tags of type c (c = 2, 3), recovered from fish released in year Y, in area A, of age a, recaptured in area i, at time t
Data	
$L^{o}_{c,Y,a,A,b}$	Observed number of tags released, tag type c, year Y, age a, release area A. An additional subscript is added for pop-up tags programmed to pop off in the bth quarter after release.
$C^{o}_{1,Y,a,A,i,b,d}$	Observed number of pop-up tags that successfully transmit stored data that were released in year Y, in area A, reside in area i, after d quarters that were programmed to release in the bth quarter at liberty
$C^{o}_{c,Y,a,A,i,t}$	Reported number of tags of type c (c = 2, 3), recovered from fish released in year Y in area A, of age a, recaptured in area i, at time t
Model parameters	
$P_{a,i}$	Probability that a fish of age a stays in area i for a quarter
$T^{*}_{a,i,j,d}$	Movement rate of fish of age a from area i to area j or staying in the same area (in the case of j = i) within the first d quarters of the year
$T_{a,i,j}$	Movement rate of fish of age a from area i to area j or staying in the same area (in the case of j = i) in a year
$F_{a,i,t}$	Instantaneous fishing mortality rate for fish of age a in area i at time t
$F'_{Y,a,i,t}$	Instantaneous fishing mortality rate for fish released in year Y in area i at time t for fish of age a
Ffy_i	Degree of mixing of newly tagged fish in the release year in area i
M_a	Instantaneous natural mortality rate at age a
$Mini$	Tag-induced mortality rate in releasing tagged fish
$R_{c,i,t}$	Reporting rate by tag type c, area i, time t
$O_{b,d}$	Probability that a pop-up tag programmed to release in quarter b releases its stored data in quarter d
B	Relative pop-up probability of earlier quarters and a later quarter to the quarter of programmed pop-up date. These resultant pdfs are used for priors for $O_{b,d}$
W_c	Probability in a year that a tag does not shed or malfunction for tag type c in a quarter (c = 1) and a year (c = 2, 3)
$\varepsilon_{1,a,t}$	Process error deviation in survival for tag type 1, age group a, time step t
$\varepsilon_{c,a,i,t}$	Process error deviation in survival for tag type c (c = 2, 3), age group a, area i, time step t
$Reast$	Proportion of the archival tag reporting rate in the east in 2006 relative to the archival tag reporting rate in the west in 2006
$Rcon_{i,t}$	Proportion of the conventional tag reporting rate relative to the archival tag reporting rate in area i, time t
$H_{a,i,t}$	Harvest (exploitation) rate for fish of age a, area i, time t
$Rdrop_i$	Drop rate of archival tag reporting rate from 2005 to 2006 in area i

treated as a single population. Explanations for all symbols (indices, model variables, data, model parameters) used for this analysis are provided (Table 2).

Movement

For a fish of age a released in area i, there is a probability that it remains in its area i of residency for a three-month period (i.e., quarterly time step), $P_{a,i}$. If fish moving to another area j do not return within the year, the expected rate of transfer $T^{*}_{a,i,j,d}$ from area i to area j within d seasons of fish of age a is thus given by

$$(1)\qquad T^{*}_{a,i,j,d} = 1 - (P_{a,i})^{d}$$

The annual movement rate $T_{a,i,j}$ from area i to area j for fish of age a and the proportion staying in the same area i applied for archival and conventional tag models is also given by

$$(2)\qquad T_{a,i,j} = T^{*}_{a,i,j,4}$$

$$(3)\qquad T_{a,i,i} = 1 - T^{*}_{a,i,j,4}$$

Capture of pop-up tag data (tag type: c = 1)

For pop-up satellite tags, the quarter (d) in which the tag records are obtained is taken into account, such that the number of pop-up satellite tag reporting events is predicted separately for quarters 1 to 4. Satellite retrieval of data for pop-up satellite tags occurs within 9 months for all deployments. Therefore, a recapture model that accounts for a quarterly time step within each year is applied to the pop-up satellite tag data. The predicted number of pop-up satellite tags $C^{p}_{1,Y,a,A,i,b,d}$ attached to fish of age a that successfully transmit stored data that were released in year Y in area A, reside in area i, after d quarters that were programmed to release in the bth quarter at liberty is given by

$$(4)\qquad C^{p}_{1,Y,a,A,i,b,d} = L^{o}_{1,Y,a,A,b} \times T^{*}_{a,A,i,d} \times W_1^{d} \times O_{b,d} \times \varepsilon_{1,a,t}$$

where $L^{o}_{1,Y,a,A,b}$ is the number of tags released in year Y in area A attached to fish of age a programmed to release in quarter b; W_1 is the probability that a tag does not shed or malfunction in a quarter; $O_{b,d}$ is the probability that a tag programmed to release in quarter b pops-off in quarter d; and $\varepsilon_{1,a,t}$ is a process error term depending on age a and yearly time t (= $Y + d/4$). The information available in the pop-up satellite tag records does not in all cases enable a verifiable elucidation of a pop-off event as a fishing mortality, natural mortality, or release from a live fish. Thus, modeling each of these events explicitly would make the estimation model more complicated without the data needed to support this. Instead, we introduced a slightly phenomenological parameter, $O_{b,d}$.

Catch and cohort equations for archival (c = 2) and conventional (c = 3) tag modeling

In the archival tag model, Fs from 1997 to 2006 are estimated, and in the conventional tag model, Fs from 1990 to 2006 are estimated. When time $t = Y$ (i.e., the year in which the tag group was released), the number of fish $N^{*}_{c,Y,a,A,i,t}$ carrying tag type c (2, archival tag; 3, conventional tag), of age a, released in year Y, in area A, moving to (or staying in) area i is given by

$$(5)\qquad N^{*}_{c,Y,a,A,i,Y} = L^{o}_{c,Y,a,A} \times (1 - Mini) \times T_{a,A,i} \times W_c$$

where $L^{o}_{c,Y,a,A}$ is the number of tags released of tag type c in year Y in area A attached to fish of age a; $Mini$ is the tag-induced mortality in releasing tagged fish; and W_c is the probability that a tag (type c) does not shed or malfunction in a year. When $t > Y$, this number of tagged fish is given by

$$(6)\qquad N^{*}_{c,Y,a,A,i,t} = [N_{c,Y,a,A,j,t} \times T_{a,j,i} + N_{c,Y,a,A,i,t} \times T_{a,i,i}] \times W_c$$

where $N_{c,Y,a,A,i,t}$ is the number of fish carrying tag type c released in year Y in area A of age a and present in area i at time t.

The predicted number of tags $C^{p}_{c,Y,a,A,i,t}$ of tag type c recovered from fish released in year Y in area A of age a, recaptured in area i in time t is given by

$$(7)\qquad C^{p}_{c,Y,a,A,i,t} = N^{*}_{c,Y,a,A,i,t} \times \frac{F'_{Y,a,i,t}}{(M_a + F'_{Y,a,i,t})} \times (1 - e^{-(M_a + F'_{Y,a,i,t})}) \times R_{c,i,t}$$

where $F'_{Y,a,i,t}$ denotes the instantaneous fishing mortality rate at age a for fish released in year Y recaptured in area i in time t; M_a is the instantaneous natural mortality rate at age a; and $R_{c,i,t}$ is the reporting rate of recaptured tags of type c in area i in time t. Hilborn (1990) utilized fishing effort data as a covariate to estimate Fs. This analysis, however, does not incorporate such information because there exist no long-term reliable effort data for Atlantic bluefin tuna fisheries. F for newly tagged fish is assumed to be lower in the first year than afterwards by a fraction Ffy, as the result of incomplete mixing, because the number of recaptures in the first year is significantly lower than expected. Thus, Ffy is less than 1.

$$(8)\qquad F'_{Y,a,i,t} = Ffy_i \times F_{a,i,t} \quad \text{for } t = Y$$

$$(9)\qquad F'_{Y,a,i,t} = F_{a,i,t} \quad \text{for } t > Y$$

where $F_{a,i,t}$ is the instantaneous fishing mortality rate at age a in area i in time t and Ffy_i is the degree of mixing of newly tagged fish in the release year in area i. The reporting rate for conventional tags is assumed to be lower than that of archival tags in each area.

$$(10)\qquad R_{3,i,t} = Rcon_{i,t} \times R_{2,i,t}$$

where $Rcon_{i,t}$ denotes a proportion of the conventional tag reporting rate relative to the archival tag reporting rate in area i, time t. $Rcon_{i,t}$ is less than 1.

The update of the abundance of tagged fish between time t and time $t + 1$ is given by

$$(11)\qquad N_{c,Y,a+1,A,i,t+1} = N^{*}_{c,Y,a,A,i,t} \times e^{-(M_a + F'_{Y,a,i,t})} \times \varepsilon_{c,a,i,t}$$

where $\varepsilon_{c,a,i,t}$ is the process error deviation in survival for tag type c at age a in area i in time t.

Process error

Process errors represent deviations in state variables from model predictions in each time step. Relatively low prior variance is assigned to process error for the probability that a tag does not shed or malfunction (W) in the pop-up tag model and natural and fishing mortality rates (Z) in the archival and conventional models. The prior for standard deviation in process error is set at 2.5% per quarter for the pop-up satellite tag model and 10% per year for the archival and conventional tag models. The amount of process error for the pop-up satellite tag model depends on the period at liberty, e.g., tags that are at liberty for one quarter have larger process errors than those at liberty for three quarters. We could have added process error in different places in the archival and conventional tag models but doing so effectively increases the number of parameters estimated and adds to computational burden. We thus included one process error term at the end of the year (eq. 11) and chose to keep it separate from the observation error that was associated with eq. 7, which predicts the number of tags returned.

Table 3. Lists of prior pdfs and fixed default values used for this analysis.

Parameter	No. of parameters	Distribution	Source of origin
Pop-up tag model			
$P_{a,i}$	4	Beta(1, 1)	
$O_{b,d}$	14	Dirichlet	
B	1	Uniform(1, 2)	
W_1	1	Beta(1, 1)	
Archival tag model			
$T_{a,i,j}$	4	Beta	Posterior of pop-up tag model
M_a	1	Lognormal(0.14, 0.1^2)	Mean from assumption used for ICCAT stock assessment (2007)
$F_{a,i,t}$	36	Lognormal($F_{a,i,t}$, 0.8^2)	Mean from estimates by ICCAT stock assessment (2007)
Ffy_i	2	Beta(1, 1)	
W_2		0.95	
$Mini$		0.1	
$R_{2,i,t}$		0.7	
$R_{2,1,2006}$	1	Beta(1, 1)	
$Reast$	1	Beta(1, 1)	
Conventional tag model			
$T_{a,i,j}$	6	Beta	(ages 0–3) posterior of archival tag model for ages 4–8 (ages 4–8 and 9+) posterior of archival tag model
M_a	1	Lognormal	Posterior of archival tag model
$F_{a,i,t}$	96	Lognormal	(ages 0–3) mean from estimates during 1990–2006 by ICCAT stock assessment (2007) (the variance is 0.8^2) (ages 4–8 and 9+) posterior of archival tag model during 1997–2006. Mean from estimates during 1990–1996 by ICCAT stock assessment (2007) (the variance is 0.8^2)
Ffy_i	2	Beta	Posterior of archival tag model
$Rcon_{i,t}$	4	Beta(1, 1)	
W_3		0.95	
$Mini$		0.1	

A symmetric uniform distribution around 1 is proposed for the process error in survival rates. Michielsens et al. (2006) found that a uniform density function is computationally more efficient than permutations of lognormal process error terms. This specification for the process error intervals is sensible, provided that it does not permit the number of tags to increase between time steps, i.e., in the case of archival and conventional tag models, the product of the total survival rate e^{-Z} and the process error should be smaller than 1. Therefore, the process error in each year will be estimated in a range larger than 0 and smaller than e^{Z} as an additional constraint.

Observation model

Observation error is modeled using a negative binomial distribution as a general form. For simplicity in terms of model stability and computational burden, the Poisson distribution is used in this analysis. The Poisson distribution is an extreme form of negative binomial distribution; the observation error variance equals the model prediction for returned tag numbers.

$$(12)\qquad C^{o}_{c,Y,a,A,i,b,d} \sim \text{Poisson}(C^{p}_{c,Y,a,A,i,b,d}) \quad \text{for } c = 1$$

$$(13)\qquad C^{o}_{c,Y,a,A,i,t} \sim \text{Poisson}(C^{p}_{c,Y,a,A,i,t}) \quad \text{for } c = 2, 3$$

Prior probability density function (pdf)

Prior pdfs of estimated parameters were set for the base-case scenario as follows (Table 3). Furthermore, for some parameters, alternative specifications for priors were examined as sensitivity tests, which are described below.

Pop-up satellite tag model

In the current analysis, a non-informative prior pdf, Beta(1, 1), is used for age-specific movement rates. This prior represents a uniform distribution between 0 and 1. The fraction of tags within a quarter that do not fail or shed, W, is also estimated using the non-informative prior pdf. Many pop-up satellite tags release prior to their programmed release time. Attachment failure has many sources but includes pin breakage, nose-cone failure, tether wearing, dart dislodging, natural mortality, and predators biting off the tags. Thus, the recovery chance of information $O_{b,d}$ is presumed to be nonzero in all quarters before the planned quarter of detachment but nonzero only for one quarter after its programmed date. The Dirichlet distribution is assumed as the prior pdfs. The prior expectation for pop-up satellite tag recovery is the highest in the quarter of programmed date and $1/B$ times as likely in each earlier quarter and a later quarter, where B is a hyperparameter of the Dirichlet distribution. For example, when B = 2 and the tag detachment is programmed in the third quarter, a relative pop-up probability is 0.111, 0.222, 0.444, and 0.222 in the first, second, third, and fourth quarters, respectively. B is an estimated parameter. The prior pdf of B is Uniform(1, 2).

Archival tag model

Stock assessment for Atlantic bluefin tuna is conducted by ICCAT using a VPA-type model (ICCAT 2007). The ICCAT assessment has a different assumption on the movement from our model (no transoceanic migration), and growing evidence suggests that this assumption is not appropriate (e.g., Block et al. 2001, 2005). This does not imply that ICCAT's assessment results are biased, because ICCAT's model explains a variety of fishery-related data such as catch per unit effort (CPUE). Thus, the fishing mortality rate estimate, depending on age and year, is used as a mean value of the prior, and a moderately high prior variance value (0.8^2 on the log scale) was applied. This prior setting permits the new data and model structure to update the prior. "Run3" results for the east area and "base case" results for the west area are used (ICCAT 2007). "Run3" is one of three scenarios examined in the 2006 ICCAT assessment and the results of it were investigated in detail. The mean value for M was the same as that utilized for the western management unit fish in the ICCAT stock assessment (2007), i.e., $0.14 \cdot \text{year}^{-1}$. A relatively small variance (0.1^2 on the log scale) was applied, as M is generally not treated as a highly uncertain parameter. There is no information on the degree of incomplete mixing of newly tagged fish (Ffy). Therefore, the non-informative prior, Beta(1, 1), is applied. The initial tag-induced mortality rate, $Mini$, was assumed to be $0.1 \cdot \text{year}^{-1}$. This value was arbitrarily set but did not impact greatly final results because the effect was countered by the Ffy estimate. The probability that a tag does not shed or malfunction in a year, W, was set at 0.95, which led to almost the lowest deviance information criterion (DIC). Preliminarily, sensitivity analyses showed that varying this value over realistic ranges did not influence the general results.

The posterior pdf of movement rates in the pop-up satellite tag model, approximated by the beta distribution, is used for the prior in the archival tag model. In general, the approximation was reasonably good, and complicated posteriors such as bimodal distributions were not observed. Prior correlations between parameters in the archival tag model are not considered, because posterior correlations in the pop-up satellite tag model are less than 0.01. Movement rates from east to west estimated from pop-up satellite tags attached to eastern management unit (the Mediterranean Sea) fish are applied to east-to-west movements of western management unit fish in the base-case scenario, because no other information exists and no stock structure is assumed in the present analysis.

Conventional tag model

For common parameters between the archival and conventional tag models, such as fishing mortality rates, movement rates, and mixing rates of newly tagged fish (Ffy), posterior distributions of the archival tag model are used as priors of the conventional tag model. Parameters in the interval (0, 1) are modeled using the beta distribution; other parameters are represented by the lognormal distribution. None of the posterior distributions obtained from the archival tag model deviated noticeably from these two distributions. Prior correlations between parameters in the conventional tag model are not considered because posterior correlations in the archival tag model are generally small and the highest value is about 0.4.

In terms of model structure, the conventional tag model expands the archival tag model to include younger fish (ages 0–3) and more years (1990–1996). Thus, new priors for F and movement rates are described (Table 3).

Base-case scenario and sensitivity analysis

Base-case scenario

The following assumptions are incorporated for the base-case scenario set as a standard basis for examining model sensitivity to different assumptions. Thus, it is not to say that the base-case results are the most plausible. (*i*) Age-specific movement rates and fishing mortality rates apply to three age groups: ages 0–3, ages 4–8, and ages 9+. A two-age-group model (ages 0–8 and ages 9+) was also examined. The goodness of fit of this model to the data, however, was much worse than that of the three-age-group model. In this study, archival and pop-up satellite tags were only attached to fish over age 4. Thus, parameters for ages 0–3 were estimated from conventional tag data only. (*ii*) Archival tag reporting rates during 1997–2005 were fixed at 0.7 in both areas. On the other hand, the 2006 reporting rate was estimated so as to satisfy the condition that F in 2005 was equal to F in 2006. Additionally, the eastern reporting rate was assumed to be lower than the western rate by a fraction $Reast$.

$$R_{2,2,2006} = Reast \times R_{2,1,2006} \tag{14}$$

The prior for $R_{2,1,2006}$ and $Reast$ was set as Beta(1, 1). This constraint comes from an expert judgment based on recent differences in campaign activity for tag returns between the west and the east. It also helps to avoid possible overparameterization. (*iii*) Conventional tag reporting rates were modeled to depend on area (west and east) and time period (1990–1998, 1999–2005). This assumption that reporting rate is constant over a period of years facilitates the estimation of fishing mortality rates. For both time periods, reporting rates were assumed to be less than that for archival tags (0.7), although archival tag data were not available before 1997. The 2006 reporting rate is assumed to drop from the 2005 rate to the same degree as the drop of the archival tag reporting rate from 2005 to 2006 in area i ($Rdrop_i$) to avoid possible overparameterization. (*iv*) Fishing mortality rates in 2006 were assumed to be the same as those in 2005, because the number of tag returns in 2006 is not yet finalized.

Sensitivity analysis

Some sensitivity analyses are conducted to test the sensitivity of estimates of parameters to model assumptions (Table 4). In estimating fishing mortality rates from tagging data, one of the largest uncertainty sources is the reporting rate estimate (Martell and Walters 2002). Currently, no reliable auxiliary data, such as observer data, are available to estimate reporting rates by areas or fleets. Therefore, sensi-

Table 4. Sensitivity analysis specifications.

Scenario	Archival tag model	Conventional tag model
1	Base case: $F_{a,i,2005} = F_{a,i,2006}$, $R_{2,1,1997–2005} = R_{2,2,1997–2005} = 0.7$, $R_{2,1,2006} \geq R_{2,2,2006}$: estimation	Base case: see the section Base-case scenario
1*b*	Base case	$R_{3,1,2006}$, $R_{3,2,2006}$: estimation independent of *Rdrop*
1*c*	Base case	$R_{3,1,1990–1998} = R_{3,1,1999–2005}$, $R_{3,2,1990–1998} = R_{3,2,1999–2005}$
2	$R_{2,1,1997–2005} = R_{2,2,1997–2005} = 0.3$	Base case
3	$R_{2,1,1997–2005} = R_{2,2,1997–2005} = 0.9$	Base case
4	$R_{2,1,1997–2005} = 0.7$, $R_{2,2,1997–2005} = 0.3$	Base case
5	$R_{2,1,1997–2005} = 0.3$, $R_{2,2,1997–2005} = 0.7$	Base case
6	$R_{2,1,2006} = R_{2,2,2006}$	$R_{3,1,1990–1998} = R_{3,2,1990–1998}$, $R_{3,1,1999–2005} = R_{3,2,1999–2005}$, $R_{3,1,2006} = R_{3,2,2006}$
7	$R_{2,1,1997–2005}$, $R_{2,2,1997–2005}$: estimation ($R_{2,1,1997–2005} \geq R_{2,2,1997–2005}$)	Base case
8	$R_{2,1,2006} = R_{2,2,2006} = 0.7$, $F_{a,i,2005} \neq F_{a,i,2006}$	$R_{3,1,2006} = R_{3,1,1999–2005}$, $R_{3,2,2006} = R_{3,2,1999–2005}$ $F_{a,i,2005} \neq F_{a,i,2006}$
9	Non-informative prior for harvest rate	Base case
10	Base case	$W_3 = 0.85$
11	Age-specific M_a	Age-specific M_a
12	Less informative prior for M_a	Base case
13	Drop tag return data in 2006	Drop tag return data in 2006
14	Negative binomial likelihood	Negative binomial likelihood

tivity tests were conducted to cover a range of possible reporting rate assumptions (scenarios 1–8).

A less informative prior for fishing mortality rates was examined (scenario 9). The fishing mortality rate can be formulated using the harvest (exploitation) rate, *H*:

$$(15) \qquad F_{a,i,t} = -\ln(1 - H_{a,i,t})$$

The prior pdfs of the harvest rates were given by Beta(1.2, 1.2). This prior represents that harvest rates have high uncertainty between 0 and 1, but the probability that harvest rates are near 0 or 1 is lower.

Hampton and Kirkwood (1990) indicated that tag-shedding rates of southern bluefin tuna might be higher than our base-case assumption (0.05). Thus, a lower value of W_3 (not-shedding rate; 0.85) was examined (scenario 10). Different natural mortality assumptions were examined. Age-specific mortality rates (M_1 = 0.323, M_2 = 0.201, and M_3 = 0.113 for ages 0–3, ages 4–8, and ages 9+, respectively), which were averaged for each age group used for the eastern area in ICCAT (ICCAT 2007), were applied for both areas (scenario 11). A less precise prior on *M* (0.8^2 on the log scale) was also examined, particularly to examine influences on the estimation of *F* (scenario 12). In the base-case scenario, some assumptions were applied to estimate *F*s for 2006 because the number of tag returns in 2006 was not finalized. To examine influences of these assumptions, the archival and conventional tag return data for 2006 were left out and all parameters were estimated until 2005 (scenario 13).

To consider the possibility of overdispersion in tag returns, returns of the three tag types were assumed to be distributed according to a negative binomial distribution (scenario 14). We used the probability density of the following form (Hilborn and Mangel 1997):

$$(16) \qquad p(C^{\mathrm{o}}|\theta) = \frac{\Gamma(k + C^{\mathrm{o}})}{\Gamma(k)C^{\mathrm{o}}!}\left(\frac{k}{k + C^{\mathrm{p}}}\right)^{k}\left(\frac{C^{\mathrm{p}}}{C^{\mathrm{p}} + k}\right)^{C^{\mathrm{o}}}$$

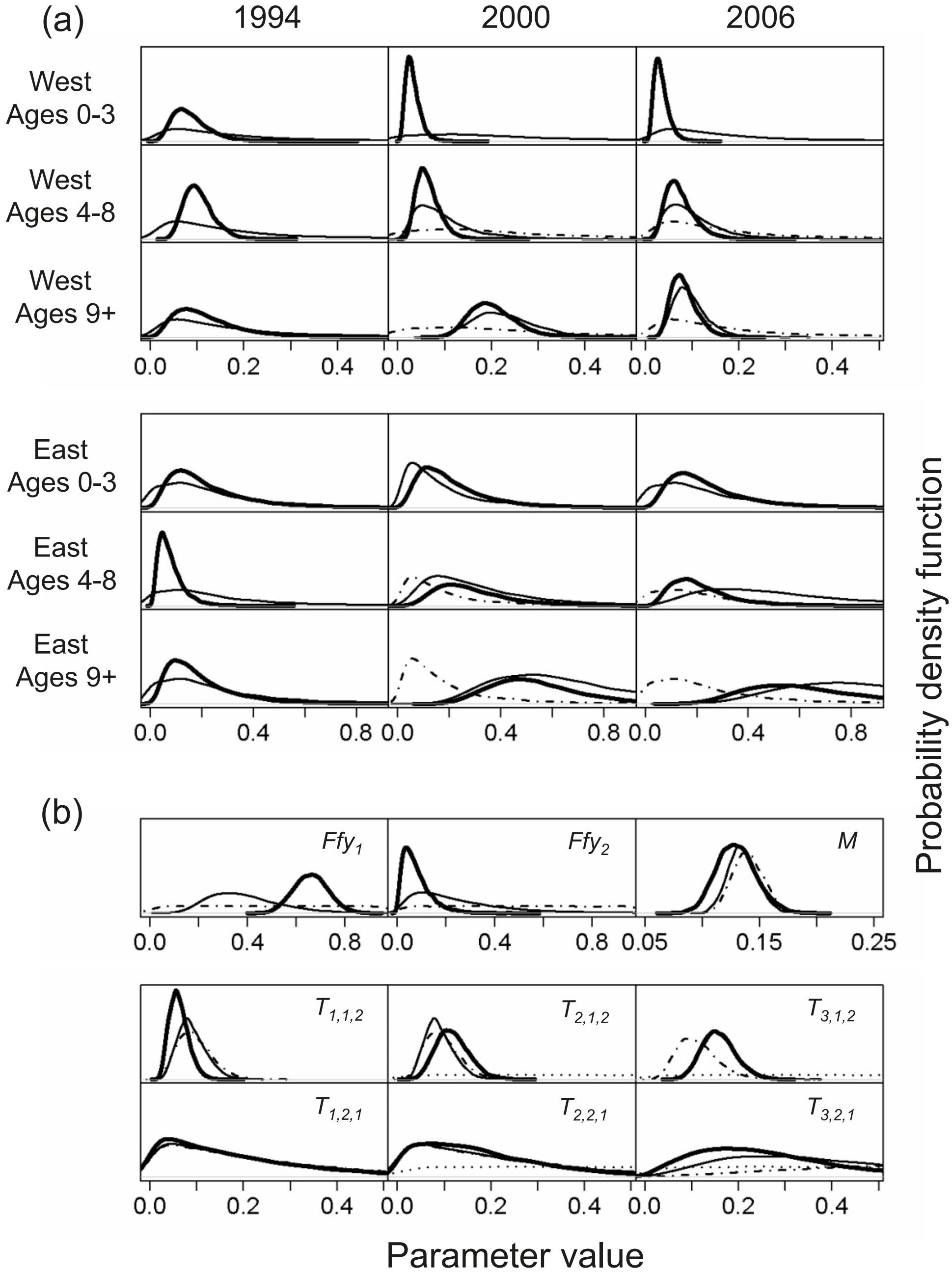
where Γ denotes the gamma function, θ represents a particular set of parameters, C^{o} and C^{p} represent the observed and predicted number of tag returns, respectively, and *k* is the overdispersion parameter. In this case, the variance in C^{o} given θ is $m + m^2/k$, where *m* represents C^{p}. *k* was assumed to be common for all data, and the prior was set as Uniform(0.1, 10) to cover moderately wide ranges.

MCMC (Markov chain Monte Carlo) modeling diagnostics

This Bayesian analysis was implemented using WINBUGS software, which has been applied successfully to mark–recapture problems similar in complexity (Michielsens et al. 2006). The comparative model fit was evaluated by DIC used for Bayesian models (Spiegelhalter et al. 2002). When the difference in DIC between models was more than 3–7, they were regarded to be "importantly" different as a rule of thumb (Spiegelhalter et al. 2002). In addition, the fit of the model to the data was assessed by comparing each data point with its posterior predictive distribution. Bayesian *p* values for observations are defined as the probability that a model-predicted data point is greater than the observed data point (Meng 1994).

Convergence diagnostics have been applied to obtain numerically stable posterior estimates. The main ones examined include the Gelman–Rubin–Brooks (BGR) plot (Best et

Fig. 2. Prior and posterior distributions of (*a*) fishing mortality rates and (*b*) other parameters (dotted line, pop-up tag model prior; dotted–dashed line, archival tag model prior; solid line, conventional tag model prior; bold solid line, conventional tag model posterior). Subscripts of parameters are defined in Table 2.



al. 1997), Monte Carlo (MC) error (standard error of the mean of the sampled values), and the comparison of the posterior distribution between the first 10% of each chain and the last 10%. The BGR plot shows the ratio of variability of the pooled chains to average variability within each chain; it should be horizontal and converge on the value of 1.0. MC error should be less than 5% of the estimated posterior SD (Gilks et al. 1995). "Burn-in" (discarding some of the initial samples from a chain; Gelman et al. 2004) was conducted to provide samples independent of initial values. Thinning (retaining simulation draws at a fixed interval and discarding the rest) was not conducted because of the low autocorrelation of Markov chains. Convergence diagnostics showed that MCMC chains had converged quickly. Therefore, the number of chains, sampling iterations, and the length of burn-in were regarded as reasonable (for detailed information, see Supplementary material available online from the NRC Data Depository).[3] It was assumed that the reported posteri-

[3] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3880. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/cms/unpub_e.html.

Table 5. Summary results for the base-case scenario.

Parameter	Age	Area	Mean (SD)	10%	50%	90%
Average fishing mortality (t: 1990–2006)						
$F_{1,1,t}$	0–3	West	0.082 (0.012)	0.067	0.081	0.098
$F_{2,1,t}$	4–8	West	0.111 (0.014)	0.094	0.111	0.130
$F_{3,1,t}$	9+	West	0.167 (0.029)	0.135	0.163	0.203
$F_{1,2,t}$	0–3	East	0.364 (0.092)	0.262	0.350	0.481
$F_{2,2,t}$	4–8	East	0.180 (0.036)	0.138	0.175	0.226
$F_{3,2,t}$	9+	East	0.330 (0.055)	0.265	0.325	0.403
Reporting rate						
$R_{3,1,1990–1998}$		West	0.232 (0.037)	0.188	0.229	0.281
$R_{3,1,1999–2005}$		West	0.112 (0.019)	0.088	0.110	0.137
$R_{3,1,2006}$		West	0.057 (0.010)	0.045	0.056	0.070
$R_{3,2,1990–1998}$		East	0.136 (0.042)	0.088	0.129	0.191
$R_{3,2,1999–2005}$		East	0.064 (0.019)	0.043	0.061	0.089
$R_{3,2,2006}$		East	0.023 (0.007)	0.015	0.022	0.031
Movement rate						
$T_{1,1,2}$	0–3	West to east	0.062 (0.020)	0.038	0.060	0.089
$T_{2,1,2}$	4–8	West to east	0.118 (0.035)	0.075	0.116	0.165
$T_{3,1,2}$	9+	West to east	0.159 (0.036)	0.114	0.156	0.206
$T_{1,2,1}$	0–3	East to west	0.185 (0.158)	0.023	0.142	0.412
$T_{2,2,1}$	4–8	East to west	0.184 (0.140)	0.031	0.154	0.378
$T_{3,2,1}$	9+	East to west	0.258 (0.149)	0.086	0.234	0.463
Degree of mixing						
Ffy_1		West	0.661 (0.071)	0.570	0.661	0.753
Ffy_2		East	0.079 (0.060)	0.020	0.064	0.157
Natural mortality						
M			0.136 (0.012)	0.121	0.136	0.152

Note: Subscripts of parameters are described in Table 2.

ors were representative of the underlying stationary distributions.

Results

Bayesian parameter update in the sequential analysis

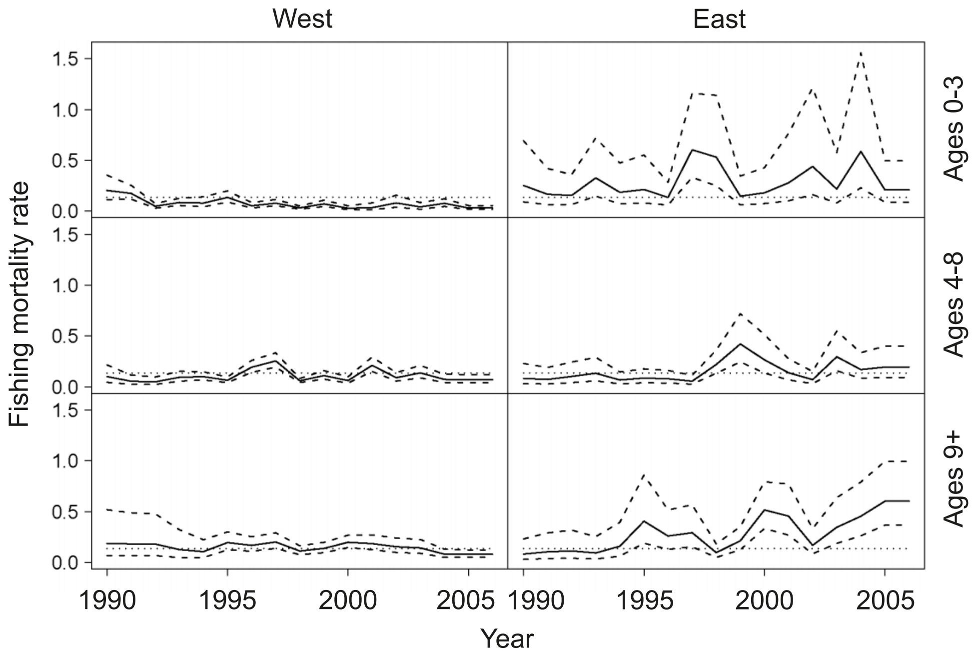
Most of the parameter estimates were updated successively throughout the sequential analysis and with the increases in information considered (Fig. 2). Fishing mortality rates (Fs) were estimated more precisely than the original prior for the archival tag model, indicating that archival and conventional tag data together can provide useful information about Fs. In particular, recent Fs for ages 4–8 and 9+ in the west were substantially updated because there were plenty of tags of both types placed on these age groups. The estimation of western Fs at ages 0–3 was improved because of the numerous conventional tag releases included in this analysis. Generally, F estimates in the east or in the early period had large uncertainties due to fewer tag releases. In some cases (e.g., eastern F for ages 4–8 in 1994), however, tagging data, especially conventional, made Fs more informative in the current analysis.

Final posteriors for movement rates (T) were more precise than non-informative priors (Fig. 2) when using results from the pop-up satellite tag model, particularly for west to east movement, partly because there are many pop-up satellite tag recoveries. They were slightly updated afterwards through archival and conventional tag models. Mixing rates of fish tagged and fish targeted by fisheries in the release year (Ffy) indicated different features between the two areas, which might reflect differences in the spatiotemporal matching among age-specific fish behaviors, fishing operations, and tag deployment places (Fig. 2). In the west, the posterior means for mixing rate parameters (Ffy) in the conventional tag model were considerably higher than the prior means, i.e., based on the posterior obtained from the archival tag model. On the other hand, the final estimate in the east was very low. The M estimate showed almost the same posterior density distribution as that of the prior, as the prior precision was set high. Summary results for the base case of the pop-up satellite tag model and the archival tag model are provided (Appendix A, Tables A1 and A2 and Fig. A1).

Results for the base-case scenario

Average F estimates between 1990 and 2006 for the three age groups were on the order of 0.08 (standard deviation, SD = 0.01) (ages 0–3) to 0.17 (SD = 0.03) (ages 9+) in the west (Table 5). F estimates for juvenile fish showed no increasing or decreasing trends from 1990 to the present (Fig. 3). Although F estimates of ages 0–3 were relatively low, the 80% probability intervals for F for ages 4–8 and 9+ overlapped with that for M. The F estimates for western fish were more precise than those for eastern fish, as more data were available for these age groups. Average Fs were from 0.18 (SD = 0.04) (ages 4–8) to 0.36 (SD = 0.09) (ages 0–3) in the east (Table 5; Fig. 3). They were about 60%–340% higher than those of the west. In the east, Fs for ages 4–8 and 9+ have increased since the late 1990s, although

Fig. 3. Posterior distribution of fishing mortality rates of each age group and area from the conventional tag modeling. Solid line represents the posterior median. Broken lines represent the 10th and 90th percentiles of the posterior. The dotted line represents the posterior median of the natural mortality rate.



uncertainty in the estimates was relatively high because of a small number of returns.

Estimates of conventional tag reporting rates after 1999 were 0.11 (SD = 0.02) in the west and 0.06 (SD = 0.02) in the east (Table 5). They were about half of those in the early time in both areas (0.23 (SD = 0.04) in the west and 0.14 (SD = 0.04) in the east). This reporting rate drop led to higher F estimates.

The estimates of movement rates from the west to east were mostly consistent with general conclusions of Block et al. (2005) about crossover rates depending on size, i.e., crossover rates are higher for larger fish (Table 5). Annual movement rate estimates (west to east) varied from 6.2% (SD = 2.0%) for fish of ages 0–3 to 11.8% (SD = 3.5%) for fish of ages 4–8 and 15.9% (SD = 3.6%) for fish of ages 9+. The estimates of east-to-west movement rates were much less precise than the west-to-east movement rates: 18.5% (SD = 15.8%) at ages 0–3, 18.4% (SD = 14.0%) at ages 4–8, and 25.8% (SD = 14.9%) at ages 9+.

The goodness of fit of the model to the observed data appeared to be acceptable (Fig. 4). Many of the observed data were included within 10% to 90% of the estimated posterior distribution. In general, posterior correlations between estimates were low. This indicates that parameters can be estimated without confounding. Movement rates, reporting rates, and fishing mortality rates show some correlation, although the correlation was <0.5.

Sensitivity analysis results

The estimated F in 2005 and 2006 was slightly lower when conventional tag reporting rates in 2006 were estimated, independent of the drop rate of archival tag reporting rates (scenario 1*b*). The differences, however, were small (e.g., $F_{2,1,2006}$ = 0.072 (SD = 0.032) for scenario 1*b*, 0.076 (SD = 0.033) for the base case). Under the assumption that reporting rates did not change over time, F estimates in the early period were higher than the base case, but those in the recent period were lower than the base case (scenario 1*c*; Fig. 5*a*). The goodness of fit of the model, however, was worse (Table 6).

With higher fixed values for archival tag reporting rates, Fs estimated from conventional tag modeling were generally lower (scenarios 2 and 3; Table 6; Fig. 5*b*). These differences, however, were not statistically significant, i.e., 95 percentiles of probability distributions of parameter estimates overlapped. DIC also showed that the goodness of fit was not different among these scenarios. Moreover, the presumed differences in archival tag reporting rate between areas did not significantly impact F estimates, although reporting rates and movement rates changed slightly (scenarios 4 and 5; Table 6). When the same reporting rates were applied to both areas (scenario 6), movement rates were different from those for the base-case scenario, but not significantly so. F estimates were identical. When archival tag reporting rates were estimated (0.74 in the west and 0.62 in the east; scenario 7; also see Appendix A, Table A2), these estimates did not significantly impact the final results of the conventional tag model. Ignoring the high uncertainty in tag return numbers in 2006 and assuming the same reporting rate in 2006 as that in 2005 (scenario 8), Fs in 2006 dropped as expected (e.g., $F_{2,1,2006}$ = 0.058 (SD = 0.034)). These results for scenarios 2 to 8, in addition to scenario 1, indicate that time trends of Fs are considerably robust to uncertainties in archival tag reporting rates. Another characteristic was that only a small number of specific parameters did not change significantly. Rather, many parameters were changed slightly at the same time.

The alternative F priors did not have a large impact on recent F estimates in the west (scenario 9; Table 6;

Fig. 4. Observed (○) and predicted (lines) distribution of the number of conventional tag returns released from 1995 to 1998, when many tags were released. The solid line represents the posterior median of expected number of tag returns. Broken lines represent the 10th and 90th percentiles of the posterior.

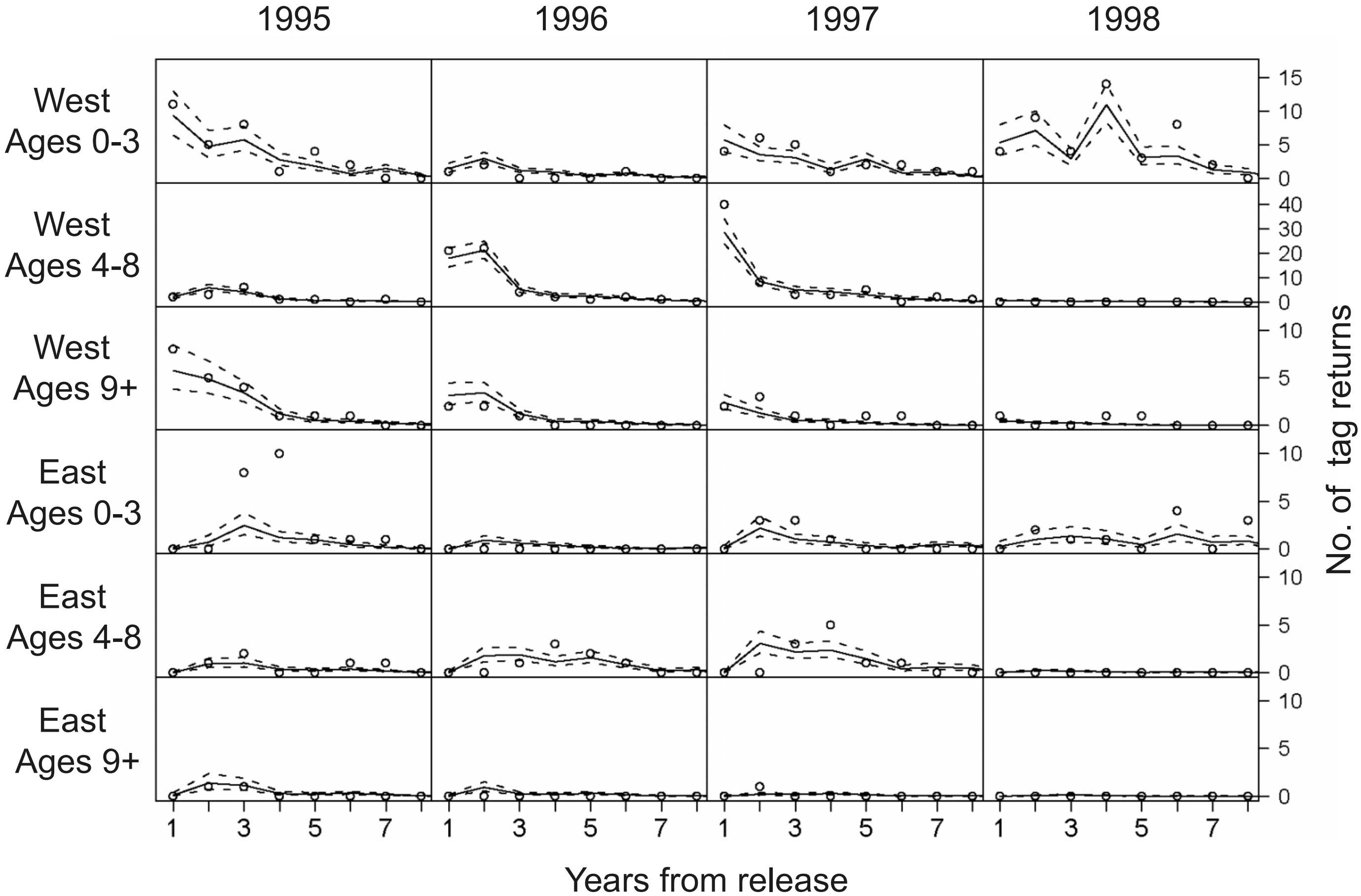


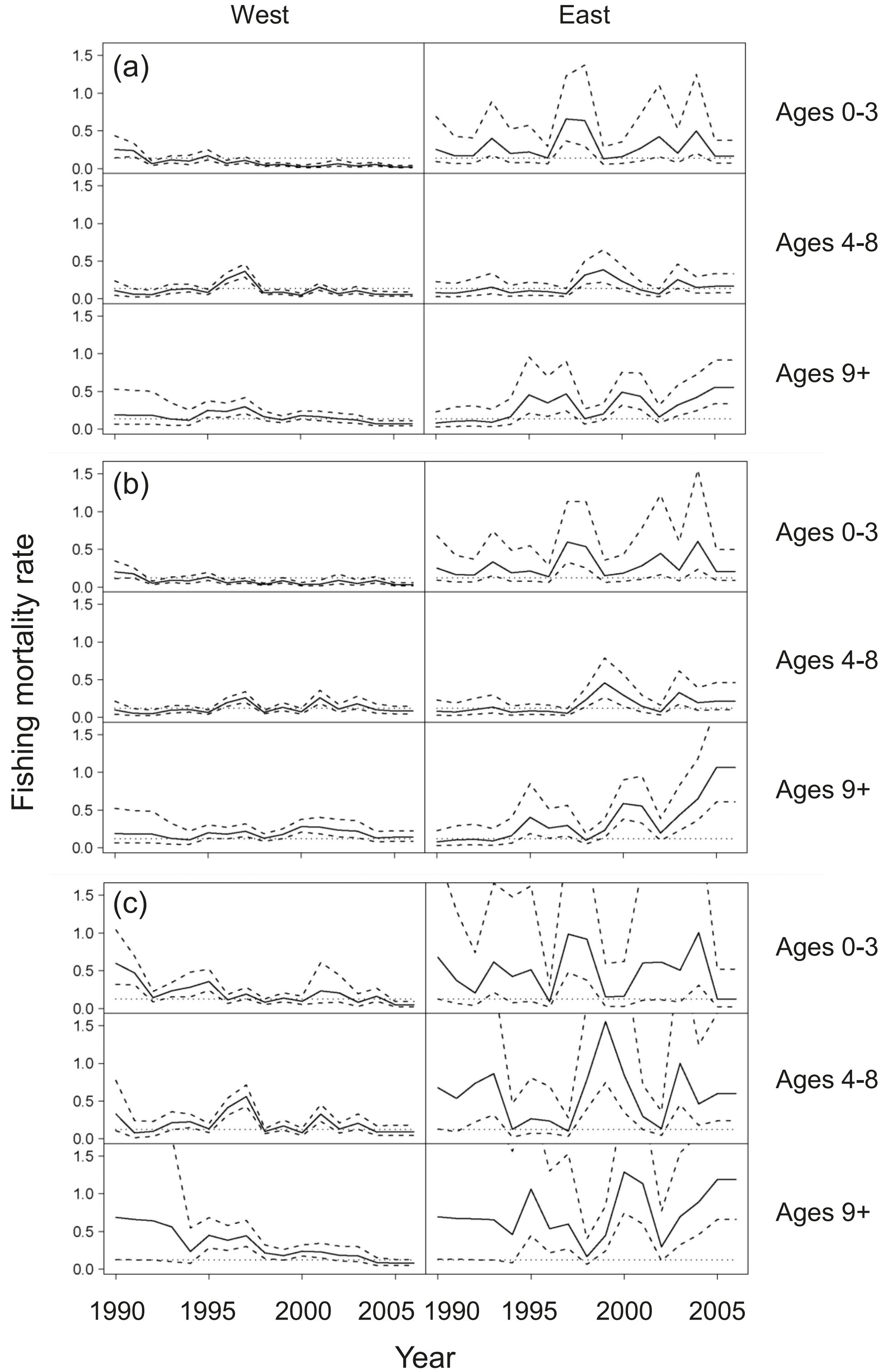
Fig. 5*c*). This indicates that the tagging data updated prior information considerably. On the other hand, priors for *F* significantly influenced results for ages 4–8 and 9+ in the east, and the estimates were only moderately updated due to relatively sparse data. The higher tag shedding rate gave poor fits to the data (scenario 10). Although this assumption estimated higher reporting rates, *F* estimates were not significantly different. Age-specific natural mortality rates did not impact *F*s and movement rates (scenario 11). DIC did not support this assumption of age-specific *M*s. When the less informative *M* prior was used, the final *M* estimate had larger variance (M = 0.118 (SD = 0.031); scenario 12). Correlations with *F*s were still low, although moderately high correlations (about 0.4) with reporting rates were observed. Incorporation of the 2006 data often led to slightly lower *F*s in 2005, e.g., *F* for ages 9+ in the west was 0.094 (SD = 0.033) in scenario 13, whereas in the base case, *F* was 0.084 (SD = 0.028). Exclusion of the 2006 data did not impact other parameters. When considering overdispersion with negative binominal likelihood, the pop-up tag model showed a much better fit to the data and movement rates had slightly larger uncertainty (scenario 14; Appendix A, Table A1). In the archival and conventional tag models, however, parameter estimates were not significantly different, and the model fit to the data was almost same.

Discussion

Advantages of Bayesian approach to integrate multiple tagging data

Bayesian state–space models can evaluate parameter uncertainties based on the amount of information available by accounting for process and observation errors explicitly (Millar and Meyer 2000; Punt 2003; Michielsens et al. 2006). Bayesian methods also provide a statistically rigorous framework with which to integrate various data sources and knowledge sequentially, following the main concept of Bayesian inference, i.e., that information is updated with new data. In this framework, parameters of interest can be estimated in a conceptually consistent and computationally feasible manner, with a single estimation model formulated for each major component of the estimation problem, although this study requires that posterior distributions can be approximated by parametric distributions. The updating of posterior pdfs as shown herein indicates that the sequential approach functions well in the estimation of fishing mortality and movement rates by combining data from three different types of tags. Michielsens et al. (2008) applied the sequential approach to the stock assessment for Baltic salmon. They estimated stock abundance trends by combining a wide range of results and information from other analyses,

Fig. 5. Posterior distribution of fishing mortality rates of each age group and area for (*a*) scenario 1*c*, (*b*) scenario 2, and (*c*) scenario 9. The solid line represents the posterior median. Broken lines represent the 10th and 90th percentiles of the posterior. The dotted line represents the posterior median of the natural mortality rate.



such as stock–recruit relationship, exploitation rates, and natural mortality. In general, each data source used for stock assessment is sparse. Therefore, it is important to synthesize many kinds of data to better understand the stock status (Punt and Hilborn 1997). Bayesian sequential estimation provides a rigorous methodology for such situations.

The present tagging models also show that there is a synergy in combining fishery-independent tag information (e.g.,

Table 6. Summary results of sensitivity tests (mean values of parameter estimates).

	Age	Area	Scenario														
			1*b*	1*c*	2	3	4	5	6	7	8	9	10	11	12	13	14
DIC			1615.6	1624.1	1616.1	1614.9	1614.0	1617.0	1614.5	1614.8	1617.1	1629.5	1622.8	1629.9	1614.7	1564.6	1617.5
n			111	107	109	109	109	109	107	109	115	109	109	111	109	109	110
Parameter																	
Average fishing mortality (t: 1990–2006)																	
$F_{1,1,t}$	0–3	West	0.081	0.092	0.085	0.080	0.079	0.086	0.089	0.080	0.083	0.222	0.073	0.080	0.083	0.086	0.086
$F_{2,1,t}$	4–8	West	0.111	0.119	0.127	0.105	0.111	0.128	0.119	0.110	0.114	0.211	0.105	0.115	0.111	0.117	0.109
$F_{3,1,t}$	9+	West	0.166	0.180	0.206	0.156	0.170	0.204	0.174	0.166	0.168	0.394	0.163	0.162	0.164	0.172	0.170
$F_{1,2,t}$	0–3	East	0.364	0.358	0.365	0.364	0.362	0.370	0.358	0.363	0.385	0.656	0.361	0.370	0.366	0.368	0.379
$F_{2,2,t}$	4–8	East	0.178	0.178	0.195	0.175	0.189	0.184	0.175	0.181	0.180	0.790	0.180	0.188	0.178	0.181	0.179
$F_{3,2,t}$	9+	East	0.327	0.342	0.427	0.308	0.400	0.351	0.313	0.341	0.316	0.919	0.325	0.324	0.323	0.310	0.339
Reporting rate																	
$R_{3,1,1990–1998}$		West	0.234	0.169	0.215	0.240	0.251	0.203	0.199	0.239	0.234	0.117	0.308	0.273	0.221	0.233	0.238
$R_{3,1,1999–2005}$		West	0.111	0.169	0.091	0.121	0.122	0.084	0.093	0.116	0.104	0.073	0.161	0.133	0.109	0.110	0.109
$R_{3,1,2006}$		West	0.101	0.086	0.074	0.055	0.053	0.077	0.040	0.055	0.104	0.035	0.082	0.068	0.053	0.056	0.056
$R_{3,2,1990–1998}$		East	0.139	0.081	0.115	0.148	0.099	0.154	0.199	0.126	0.141	0.156	0.210	0.161	0.130	0.136	0.125
$R_{3,2,1999–2005}$		East	0.065	0.081	0.052	0.071	0.044	0.075	0.093	0.059	0.062	0.095	0.112	0.078	0.062	0.063	0.063
$R_{3,2,2006}$		East	0.069	0.029	0.029	0.023	0.028	0.022	0.040	0.023	0.062	0.032	0.040	0.028	0.021	0.022	0.022
Movement rate																	
$T_{1,1,2}$	0–3	West to east	0.061	0.072	0.070	0.058	0.083	0.053	0.045	0.066	0.058	0.042	0.051	0.060	0.063	0.064	0.064
$T_{2,1,2}$	4–8	West to east	0.118	0.124	0.127	0.112	0.152	0.104	0.091	0.127	0.119	0.055	0.109	0.121	0.119	0.120	0.129
$T_{3,1,2}$	9+	West to east	0.156	0.164	0.183	0.149	0.196	0.149	0.142	0.165	0.154	0.132	0.154	0.157	0.156	0.156	0.164
$T_{1,2,1}$	0–3	East to west	0.190	0.166	0.181	0.187	0.164	0.201	0.220	0.181	0.195	0.202	0.212	0.190	0.184	0.187	0.205
$T_{2,2,1}$	4–8	East to west	0.194	0.167	0.180	0.192	0.149	0.225	0.286	0.181	0.195	0.445	0.242	0.207	0.181	0.190	0.220
$T_{3,2,1}$	9+	East to west	0.265	0.233	0.243	0.275	0.195	0.303	0.401	0.241	0.261	0.672	0.308	0.262	0.266	0.275	0.259
Degree of mixing																	
Ffy_1		West	0.661	0.667	0.730	0.636	0.641	0.748	0.688	0.658	0.659	0.530	0.602	0.609	0.677	0.645	0.646
Ffy_2		East	0.078	0.087	0.088	0.075	0.086	0.078	0.070	0.081	0.080	0.042	0.065	0.070	0.081	0.077	0.079
Natural mortality																	
M			0.137	0.138	0.121	0.141	0.129	0.127	0.137	0.136	0.138	0.126	0.128		0.118	0.136	0.136
M_1														0.268			
M_2														0.195			
M_3														0.116			
Overdispersion																	
k																	4.868

Note: DIC, deviance information criterion; n, number of parameters. For the base case, DIC = 1614.8 and n = 109. The number of parameters represents all except process error terms. Standard deviations are shown in the Supplementary material (available online from NRC Data Depository).

pop-up satellite tag) with fishery-dependent tag information (e.g., archival and conventional tags). There have been numerous examples of quantitative models using tagging data to estimate parameters regarding population dynamics such as stock size, natural mortality, exploitation rates, reporting rates, and movement rates (Quinn and Deriso 1999; Walters and Martell 2004). These factors, however, tend to be confounded and it is often difficult to solve this issue. To overcome this issue, some studies have used other additional information in tagging data analyses but very few studies have applied the Bayesian approach. Polacheck et al. (2006) demonstrated that incorporation of catch-at-age data into tag-recapture analysis improves mortality estimation. Radiotelemetry information also provides more precise and unbiased mortality estimates, including reporting rate estimates (Nasution et al. 2001; Pollock et al. 2004).

It is important to note that the three kinds of tagging data in this study provided complementary information for the estimation of *F*s and movement rates to understand the entire life history of the bluefin tuna and fishery stock management. When pop-up satellite tag information was not used, statistically valid estimates could not be obtained, as movement rates had higher uncertainty and higher correlations between themselves and *F*s. This shows that pop-up satellite tag data are critical to estimating *F*s, as well as movement rates, while not providing information on *F*s themselves. Also archival and conventional tags cover different age ranges of fish tagged, which is important for estimating age-specific (size-specific) *F*s over a wider range of ages. *F* estimates for ages 9+ have larger uncertainty in the earlier 1990s compared with the later 1990s, as archival tag data were not available for the earlier time periods.

Thus far, few methodologies have been developed to estimate both movement and fishing mortality rates (Sibert et al. 1999; Hampton and Fournier 2001; McGarvey and Feenstra 2002). Fishery-independent, as well as fishery-dependent, tagging data would be useful to reduce uncertainties for movement rates, but such tagging research is still rare because of high deployment costs. The present study capitalized on the highest number of pop-up satellite tagging records yet available for fisheries analysis. Moreover, Bayesian tagging models have shown improved performance over maximum likelihood approaches, even in such cases where tagging data are relatively sparse (Chao 1989; Martell and Walters 2002). This is partly a result of incorporating additional information as a prior density function. These two factors make it possible to estimate exploitation and movement rates more precisely in this analysis of Atlantic bluefin tuna.

Estimation of reporting rates in Bayesian frameworks

Reporting rates for conventional tags can be estimated from tagging data, with an assumption regarding model structure: conventional tag reporting rates are lower than archival tag reporting rates, most likely due to the reward differences ($1000 versus a hat). Tag-recapture data can be informative about exploitation rates if recapture and reporting rates are high and the tagging program is properly designed (Martell and Walters 2002; Pine et al. 2003). The common occurrence of nonreporting of recaptured tags, however, produces large uncertainties about *F* estimates. Although tagging data by themselves contain some information on reporting rates, the information is generally weak and the estimates are unstable without auxiliary information in the framework of the maximum likelihood method (Hoenig et al. 1998; Polacheck et al. 2006). Within a Bayesian framework, these uncertainties can be incorporated into estimation models easily. Michielsens et al. (2006) set priors for reporting rates from expert opinions; however, the tagging data in their study did not update the priors for reporting rates. In the current study, instead of specifically setting the prior pdfs of reporting rate, the structural model assumption of higher archival tag reporting rates than conventional was applied, based on expert judgment. In addition, the use of informative priors for *F*s and movement rates from the archival tag model, as well as a tight prior for *M*, facilitates the estimation of conventional tag reporting rates. The significant Bayesian update of conventional tag reporting rates, irrespective of archival tag reporting rates, indicates that tag-recapture data include sufficient information on reporting rates. This is the reason that *F* estimates are relatively robust for different archival tag reporting rate assumptions. In this case, the structural assumption might not be necessary, but such assumptions could play more important roles in situations where data are sparser.

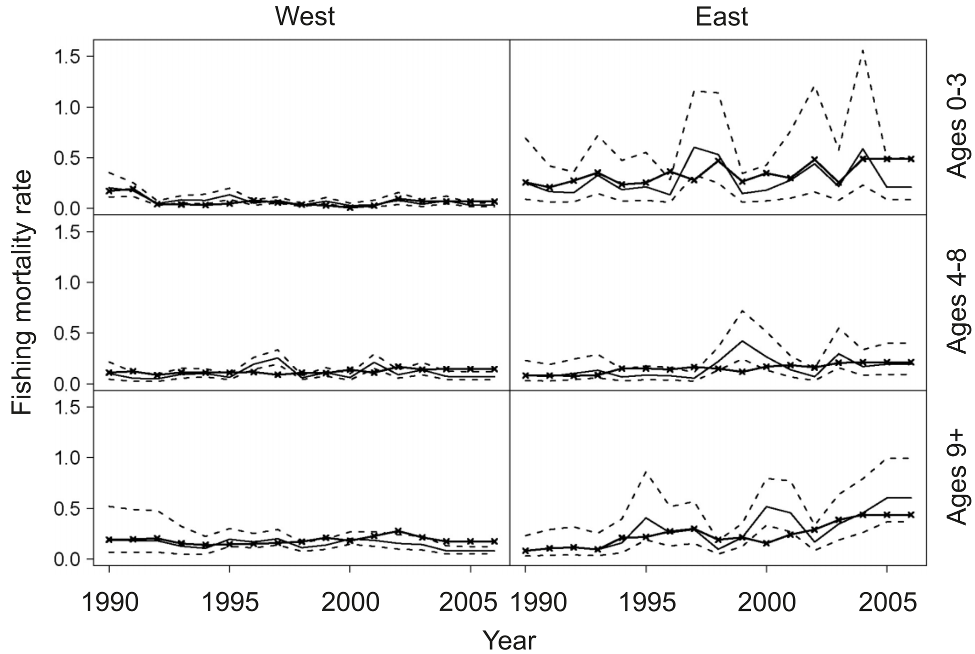
Estimated reporting rates for conventional tags are in the range of 0.06 (after 1999 in the east) to 0.23 (before 1999 in the west) for the base-case scenario. Recent rates after 1999 are half of earlier rates before 1999, and eastern rates are half of western rates. The reason for the apparent drop in reporting rates is hard to pinpoint and may be due to fluctuation in the number of releases over a given set of years prior to the recapture year and changes in fishing operations such as increased tuna penning in the Mediterranean Sea. A change in stock composition would also be plausible as a cause for changing return rates. When the tagged fish are predominantly western in origin, their interaction is with American and Canadian fleets. When fish are eastern, the number of fleets for potential recapture increases to greater than 10 and reporting rates may be lower due to lower transfer of educational information about the tag-recapture programs to some of these fleets.

Conventional tag reporting rates of longline fleets for southern bluefin tuna were estimated from observer data and port sampling in the 1990s. They ranged from 20% to 60%, though variance was relatively large (Eveson and Polacheck 2005; P. Eveson, CSIRO Marine and Atmospheric Research, Castray Esplanade, Hobart, Tasmania 7001, Australia, personal communication, 2006). Australian observers visited almost all Japanese vessels entering Australian ports to collect conventional tags in the 1990s, which supports the notion that conventional tag reporting rates here may be higher than those in Atlantic bluefin tuna fisheries. Hearn et al. (1999) point out that reporting rates might vary over years and ages. In this case, observer data would be helpful to estimate reporting rates more precisely, though they were not available for the present analyses.

Stock status, migration, and stock structure of Atlantic bluefin tuna

In general, the *F* estimates of this study overlapped the ICCAT's *F*s, which are estimated by a VPA model that

Fig. 6. Comparisons between results for the base-case scenario (solid line, posterior median; broken lines, 10th and 90th percentiles of the posterior) and ICCAT (2007) *F* estimates for Atlantic bluefin tuna (bold line with a symbol).



does not use tagging data (Fig. 6; ICCAT 2007). ICCAT's estimates of *F* are used as priors of the present analysis, which may in part explain the similarity, particularly in the east where the tag data were limited. The *F* estimates in the west, however, result from Bayesian updating with tagging data and the priors have little impact. This might indicate that tagging data have information regarding the exploitation rate consistent with the catch-at-age data and stock abundance indices used for the ICCAT stock assessment. It is interesting that the electronic tagging data, which are based mostly on deployments at a few isolated locations, should yield information so similar to the catch-at-age and stock abundance indices, which are based on fisheries that are spatially much more dispersed.

The similarity between the tagging-based estimates of *F* and ICCAT stock assessment results lend support to ICCAT's recent cautions that the current *F* levels for Atlantic bluefin tuna may not be sustainable in both areas (ICCAT 2007). The high *F* estimates for large fish (ages 4–8 and 9+) in the west since the 1990s, which are similar to the assumed natural mortality rate, indicate that fisheries might have considerably impacted fish population dynamics and reduced its resilience. Furthermore, *F* levels in the east have been higher than in the west and most likely increasing in the last decade. It might be necessary to reduce fishing effort quickly to return harvests to sustainable levels. It is, however, noted that the recent estimates of *F* in the west, especially for ages 9+ since 2002, were lower compared with ICCAT's results and the natural mortality estimate, although the difference is unlikely to be significant. These low estimates might be associated with changes in reporting rates and (or) movement rates and possible lags in the reporting and compilation of the most recently recaptured tags.

The current study analyzes extended versions of the tagging data sets evaluated in Block et al. (2005). The current study, however, attempts to reduce possible biases in movement rate estimates that may be caused by *F* differences between areas. We obtained higher estimates of movement rates from west to east than those reported by NRC (1994) (about 1%), which was based on conventional tagging data before the 1990s (Mather et al. 1995). As Block et al. (2005) point out, this potentially is associated with large fish being tagged and consistent with a two-component model for west-to-east movements with adolescent eastern-origin fish tagged in the western Atlantic returning to natal spawning grounds and large western fish moving into the central and eastern Atlantic foraging grounds. The higher estimates of movement rates in the current study might indicate that the proportion of eastern fish in the western fishery has increased over this period. Such changes in stock composition in the west could also explain the low return rates of conventional tags after the 1990s. It could be that before 1990, it was mostly western fish being tagged and western recoveries of residential fish, whereas after this period, the fraction of eastern fish in the west increased, and hence, the tagging of them has increased, as well as apparent dispersal to the east as a consequence. Consistent with this hypothesis is the observation by Block et al. (2001, 2005) that western fish tend to remain, for a significant portion of adolescent years, in the western management unit. Thus, if conventional tags were deployed on primarily adolescent western fish, results from the electronic tagging imply that they would remain primarily in the western management unit and thus would be more recoverable by local fishers. Sibert et al. (2006) also suggest that influences of oceanographic conditions in a given year might have an influence on migration patterns. These considerations suggest that one improvement of the model would be to account for stock structure, including stock origin (e.g., genetics or otoliths), stock mixing, and stock-specific movement patterns with season and environmental information.

Limitation of the current models and future research

In addition to ignoring stock structure, the current study relies on several simplifying assumptions. In some cases, the fraction of Bayesian *p* values falling between 2.5% and 97.5% was relatively small, e.g., 27% and 43% in the case that the number of observed tag returns was more than 1 and 2 (n = 265 and 92), respectively, with many values falling below 2.5%. This indicates that overdispersion occurs in the data relative to that presumed in the probability model for the data, i.e., observed variances are larger than those expected from the Poisson distribution (Hilborn and Mangel 1997). This might result from the violation of the Poisson assumptions of random sampling and complete mixing of tagged and untagged fish, which is caused by several factors such as highly selective fishing behaviors and high degree of school fidelity of fish. Moreover, the application of a negative binomial model, in which the variance can be larger than the mean, did not improve greatly the model prediction except for the pop-up tag model (the faction of Bayesian *p* values between 2.5% and 97.5% was 31% and 50% for the conventional tag model when the number of observed tag returns was more than 1 and 2, respectively). This overdispersion might be related to many "zero" return data due to the small number of tag releases and low recapture and reporting rates. In fact, almost 90% of the observed return data for each release and recapture year, age, and area was represented by zero counts. Though statistical modeling considering such overdispersion might become more complicated, zero-inflated and hurdle models may be more appropriate to analyze such zero-inflated data (Cunningham and Lindenmayer 2005; Martin et al. 2005). The overdispersion issue might lead to underestimation of parameter variances and suggests that caution be taken in the interpretation of uncertainties.

Movement rate estimates largely depend on pop-up satellite tag data. However, it is plausible that movement rates from pop-up tagged fish may be low due to the short duration of these tags and season in which these tags are installed. The present model also assumes that fish move from west to east, or vice versa, only once a year. If fish cross over frequently within a year, annual migration rates from this model are likely to be underestimated. Although evidence indicates that multiple crossings by individuals in a single year does occur, our preliminary analysis showed that return crossover rates within a year are relatively low. However, this is dependent on the length of a data record and the type of tag deployed. Short tag deployments (e.g., pop-up satellite tags) by their nature will not have the time to show multiple crossings. The analysis also assumes one aggregated fishery in each area and does not consider differences among fleets in *F*s and reporting rates. In contrast, Carruthers (2007) analyzed conventional tagging data for Atlantic swordfish using a more complicated Bayesian model and estimated exploitation rates by fleets. In addition, this model adopted the two-area model based on the ICCAT geographical delimitation. We realize, however, that in the future, finer-scale zoning will be more appropriate if proper area definitions can be determined. To estimate the migration pattern in a detailed spatiotemporal scale based on proper zoning, it will be necessary to utilize track information of pop-up and archival tags between the release and recapture points and develop a more detailed model, considering seasonal movements and including a variety of fishery-related data. Tags released from the eastern management unit also could improve parameter estimates such as east-to-west movements and *F*s in the east.

Despite some limitations in the model, this study provides the first comprehensive framework to combine multiple data sources from tagging experiments to estimate exploitation and movement rates. This methodology could be applied widely to other fish populations and species. In addition to electronic tagging, genetic and otolith microchemistry analyses have been applied to Atlantic bluefin tuna to validate and quantify the extent of mixing between the putative stocks with more precision than is currently possible. Integration of such information is essential to the understanding of temporal and spatial population dynamics of each spawning stock, their seasonal overlap, and timing of separation. Together these methods offer significant improvements in resolving long-standing issues in the fisheries management of bluefin tuna (Block et al. 2005; Fromentin and Powers 2005).

Acknowledgements

Eric Prince of the US National Marine Fisheries Service kindly provided access to the National Oceanic and Atmospheric Administration (NOAA) conventional tagging data records for Atlantic bluefin tuna. The Data Library and Archives of the Woods Hole Oceanographic Institution provided access to Frank Mather's conventional tagging data and records. Nathan Taylor provided valuable comments that improved this manuscript. Carl Walters and Rob Ahrens are thanked for their helpful discussions. Two anonymous reviewers are thanked for the comments on an earlier draft of this paper. This paper is funded by the Fisheries Research Agency (Yokohama, Japan) to H. Kurota, a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to M. McAllister, and a NOAA grant to B. Block. The Lenfest Oceans grant provided partial support for G. Lawson and S. Teo during the course of this study.

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Appendix A

Summary results for the base case of the pop-up satellite tag model and the archival tag model are provided in Tables A1 and A2 and Fig. A1, which follow.

Fig. A1. Posterior distribution of fishing mortality rates of each age group and area from the archival tag modeling. Solid line represents the posterior median. Broken lines represent the 10th and 90th percentiles of the posterior. The dotted line represents the posterior median of the natural mortality rate.

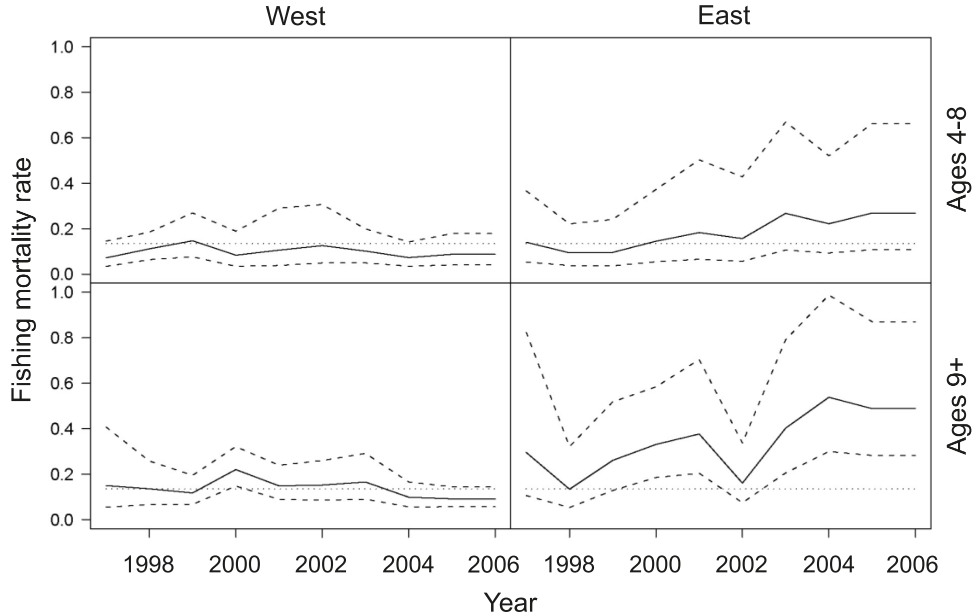

Table A1. Summary results for the pop-up satellite tag model.

			Scenario 1 (base case)	Scenario 14
Parameter	Age	Area	Mean (SD)	Mean (SD)
Movement rate				
$T_{2,1,2}$	4–8	West to east	0.096 (0.037)	0.107 (0.044)
$T_{3,1,2}$	9+	West to east	0.113 (0.043)	0.114 (0.046)
$T_{2,2,1}$	4–8	East to west	0.210 (0.170)	0.227 (0.188)
$T_{3,2,1}$	9+	East to west	0.631 (0.235)	0.631 (0.239)
Not shed or malfunction				
W			0.888 (0.029)	0.866 (0.037)
Pop-off probability prior				
B			1.377 (0.261)	1.381 (0.262)
Pop-off probability				
$O_{1,1}$			0.965 (0.020)	0.962 (0.025)
$O_{1,2}$			0.035 (0.020)	0.038 (0.025)
$O_{2,1}$			0.175 (0.053)	0.175 (0.064)
$O_{2,2}$			0.793 (0.055)	0.790 (0.066)
$O_{2,3}$			0.032 (0.021)	0.035 (0.024)
$O_{3,1}$			0.221 (0.040)	0.222 (0.053)
$O_{3,2}$			0.397 (0.047)	0.324 (0.061)
$O_{3,3}$			0.358 (0.048)	0.427 (0.066)
$O_{3,4}$			0.024 (0.014)	0.028 (0.018)
$O_{4,1}$			0.272 (0.054)	0.257 (0.063)
$O_{4,2}$			0.333 (0.057)	0.330 (0.067)
$O_{4,3}$			0.353 (0.059)	0.366 (0.071)
$O_{4,4}$			0.021 (0.015)	0.023 (0.018)
$O_{4,5}$			0.021 (0.016)	0.024 (0.019)
Overdispersion				
k				4.197 (1.735)

Note: DIC, deviance information criterion; number of parameters (n) represents all except process errors. For scenario 1 (base case), DIC = 425.4 and n = 20; for scenario 14, DIC = 406.7, n = 21.

Table A2. Summary results for the archival tag model (mean values of parameter estimates).

	Age	Area	Scenario 1	2	3	4	5	6	7	8	9	11	12	13	14
DIC			365.2	387.2	365.0	372.3	375.8	363.9	366.4	366.4	376.9	364.1	363.8	334.3	367.8
n			45	45	45	45	45	44	47	47	45	46	45	43	46
Parameter															
Average fishing mortality (t: 1997–2006)															
$F_{2,1,t}$	4–8	West	0.117 (0.029)	0.143	0.108	0.118	0.146	0.117	0.115	0.120	0.272	0.120	0.115	0.122	0.122
$F_{3,1,t}$	9+	West	0.151 (0.030)	0.227	0.131	0.157	0.224	0.152	0.149	0.150	0.222	0.156	0.143	0.156	0.158
$F_{2,2,t}$	4–8	East	0.239 (0.079)	0.259	0.233	0.253	0.244	0.238	0.242	0.232	0.816	0.241	0.238	0.231	0.237
$F_{3,2,t}$	9+	East	0.403 (0.110)	0.567	0.366	0.522	0.440	0.399	0.418	0.388	0.925	0.407	0.387	0.389	0.410
Reporting rate															
$R_{2,1,1997–2005}$		West	0.70	0.30	0.90	0.70	0.30	0.70	0.74	0.70	0.70	0.70	0.70	0.70	0.70
$R_{2,1,2006}$		West	0.36 (0.165)	0.24	0.41	0.30	0.27	0.30	0.35	0.70	0.33	0.36	0.34		0.36
$R_{2,2,1997–2005}$		East	0.70	0.30	0.90	0.30	0.70	0.70	0.62	0.70	0.70	0.70	0.70	0.70	0.70
$R_{2,2,,2006}$		East	0.25 (0.120)	0.17	0.29	0.19	0.20	0.30	0.24	0.70	0.23	0.25	0.23		0.24
Movement rate															
$T_{2,1,2}$	4–8	West to east	0.090 (0.031)	0.098	0.085	0.115	0.080	0.090	0.095	0.089	0.068	0.092	0.090	0.092	0.098
$T_{3,1,2}$	9+	West to east	0.162 (0.038)	0.187	0.152	0.205	0.149	0.160	0.170	0.158	0.135	0.162	0.158	0.157	0.166
$T_{2,2,1}$	4–8	East to west	0.204 (0.166)	0.197	0.211	0.177	0.218	0.204	0.200	0.206	0.234	0.201	0.206	0.205	0.219
$T_{3,2,1}$	9+	East to west	0.373 (0.201)	0.320	0.404	0.259	0.424	0.374	0.350	0.385	0.563	0.367	0.399	0.408	0.373
Degree of mixing															
Ffy_1		West	0.392 (0.151)	0.562	0.339	0.384	0.576	0.389	0.382	0.380	0.230	0.388	0.402	0.378	0.386
Ffy_2		East	0.247 (0.189)	0.344	0.220	0.338	0.251	0.246	0.260	0.253	0.141	0.243	0.252	0.242	0.243
Natural mortality															
M			0.136 (0.013)	0.121	0.140	0.129	0.126	0.135	0.135	0.137	0.137		0.088	0.135	0.136
M_2												0.201			
M_3												0.110			
Overdispersion															
k															6.472

Note: Standard deviations (SDs) for scenario 1 (base case) are given in parentheses after the mean. All other SDs are given in the supplementary material (available online from NRC Data Depository). DIC, deviance information criterion; number of parameters (n) represents all except process errors.