Interannual variation in large-scale movement of Atlantic bluefin tuna (*Thunnus thynnus*) determined from pop-up satellite archival tags

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Abstract: Data from pop-up satellite archival tags (PSATs) deployed on Atlantic bluefin tuna (*Thunnus thynnus*) in 1999, 2000, and 2002 were analyzed synthetically using variants of a state–space statistical model to estimate tag shedding positions, in situ position estimation errors, and movement parameters. Geographic position estimates were computed from PSAT data for 30% to 50% of the days at liberty for each tag. Such relatively low position reporting rates may present biased impressions of movement for brief times at liberty. The respective longitude and latitude errors were estimated by the state–space Kalman filter model to be approximately 0.4° and 1.0° for the 1999 deployments, 0.4° and 2.1° for the 2000 deployments, and 0.9° and 2.1° for the 2002 deployments. Estimated movement parameters were used in stochastic simulation models to predict the distribution of tagged fish after times at liberty that exceed observed reporting dates. The distributions predicted by parameters estimated from the 2002 deployments were more restricted than those estimated from the 1999 deployments. Atlantic bluefin dispersal patterns appear to be age- or size-dependent and linked to shifts in oceanographic conditions. Future fisheries management measures should address interannual differences in stock distribution identified by electronic tags.

Résumé : Nous avons analysé de manière synthétique des données enregistrées par des étiquettes satellites auto-détachables à archivage (PSATs) fixées sur des thons rouges (*Thunnus thynnus*) en 1999, 2000 et 2002 à l'aide de variantes du modèle statistique état–espace afin d'estimer les positions de libération des étiquettes, les erreurs des estimations de position in situ et les paramètres du déplacement. Nous avons calculé les estimations des positions géographiques à partir des données de PSAT pour 30 % à 50 % des jours de liberté pour chaque étiquette. De tels taux faibles de signalisation des positions peuvent donner des impressions erronées des déplacements pour les courtes périodes en liberté. Nous avons estimé à l'aide du modèle état–espace de filtre de Kalman les erreurs de longitude et de latitude qui sont respectivement d'environ 0,4° et 1,0° pour les déploiements de 1999, de 0,4° et 2,1° pour ceux de 2000 et de 0,9° et 2,1° pour ceux de 2002. Les paramètres estimés du déplacement ont servi dans des modèles de simulation stochastique à prédire la répartition des poissons marqués après des périodes de liberté qui surpassent les dates de signalisation observées. Les répartitions prédites par les paramètres estimés à partir des déploiements de 2002 sont plus restreintes que celles faites à partir des déploiements de 1999. Les patrons de dispersion des thons rouges de l'Atlantique semblent être dépendants de l'âge ou de la taille et reliés à des changements dans les conditions océaniques. Les mesures futures de gestion des pêches devraient tenir compte des différences interannuelles de répartition des stocks signalées par les étiquettes électroniques.

[Traduit par la Rédaction]

Introduction

Transatlantic movements of Atlantic bluefin tuna (*Thunnus thynnus*) have been well-documented by classical mark and recapture techniques since the 1950s (NRC 1994). Catch records from high-seas longline fishing (Wilson 1965; Shingu et al. 1975) also indicate that bluefin tuna use mid-Atlantic habitat (Lutcavage et al. 1999). Recent tagging studies using electronic tags have confirmed transatlantic movements and use of mid-Atlantic habitats (Block et al. 2001, 2005; Wilson et al. 2005). Atlantic bluefin tuna have been managed as separate stocks since the 1980s, with an arbitrary boundary at 45° W longitude. This policy is based on assumptions of low mixing rates (1%–4% annually), sepa-

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rate spawning areas, and spawning site fidelity (Sissenwine et al. 1998). A recent electronic tagging study (Block et al. 2005) concluded that bluefin tuna forage throughout the Atlantic but exhibit spawning site fidelity to either the Mediterranean or the Gulf of Mexico. However, results from other tagging studies are not entirely consistent with these conclusions (Lutcavage et al. 1999; Wilson et al. 2005), and information on the reproductive status of bluefin tuna outside of the known spawning areas is extremely limited and does not rule out other spawning areas (Richards 1976; Mather et al. 1995).

Modern electronic tagging devices offer biologists a wealth of information on movement and distribution of fishes (Arnold and Dewar 2001). Pop-up satellite archival tags (PSATs) are externally attached to fish and record time, light intensity, hydrostatic pressure, and temperature. After a preset date, the tags detach themselves from the fish, rise to the sea surface, and transmit the stored information to a central location via satellite. Daily geographic position estimates are computed from the record of light intensity. The record of water pressure and temperature provides insights into the depth associations and habitat preferences of the fish and may assist in detecting tag shedding. The utility of these devices depends on retention of the device on the fish during the time at liberty and successful transmission of data. Tag shedding is a widespread problem in all tagging studies, but is seldom discussed in the realm of electronic tagging (Holland and Braun 2003). The current generation of PSATs detect and report premature releases, but earlier models lacked this capability and also did not record pressure. Thus, detection of tag shedding in early model PSATs is difficult because ambient temperature was the only additional variable recorded by the tags. Such data, when interpreted against sea surface temperature records, do not necessariy reflect whether the tag had remained on the fish (Lutcavage et al. 1999).

Parametric representation of horizontal movement (Sibert and Fournier 2001; Sibert et al. 2003) offers the possibility of using data from electronic tags to objectively detect such changes in behavior. Statistical tests can be applied to the differences in the numerical values of parameters estimated from the horizontal movements recorded by the tags under different movement hypotheses. Such changes in movement may indicate tag shedding or actual changes in behavior, such as would be required for a fish residing in the western Atlantic to begin a transatlantic migration. In addition, the estimated movement parameters can be used to extrapolate movements of tagged fish over periods of time that exceed the duration of the attachment.

We augment the PSAT data used by Wilson et al. (2005) with earlier data from PSATs deployed on larger fish (Lutcavage et al. 2000, 2001) to explore possible interannual differences in movements of Atlantic bluefin tuna in the western Atlantic Ocean. Variants of the state–space model estimated by the extended Kalman filter (Sibert and Fournier 2001; Sibert et al. 2003) are used (*i*) to estimate in situ position estimation errors and movement parameters, (*ii*) to detect apparent changes in movement, and (*iii*) to evaluate alternative hypotheses about movement. The estimated movement parameters are applied in simple simulations, using a biased random walk model, to predict the distribution of tagged fish after times at liberty extending beyond the reporting dates. In the process of conducting this analysis, we became aware of certain practical problems with the interpretation of PSAT data. We will briefly discuss these problems and their implications for the use of PSATs for the study of large-scale fish movement.

Materials and methods

Data from PSATs deployed in 1999, 2000, and 2002 were reanalyzed. Details of deployment and attachment methods are described briefly here and in more detail elsewhere (Lutcavage et al. 1999, 2001). All deployments used PTT-100 tags from Microwave Telemetry Inc. (MWT) (Columbia, Maryland, USA). During the period from 1999 through 2002, the tag manufacturer made several improvements to both the hardware and software in the tags. Tag attachment methods were improved and deployment strategies were modified. In addition, availability of fish suitable for tagging differed because tagging was conducted from commercial fishing boats using harpoon, rod and reel, and purse seine capture methods.

In 1999 and 2000, the tags were attached to dorsal musculature of the fish using a medical-grade nylon dart and 1.68 mm monofilament fishing line. Tags were deployed on the commercial fishery size class known as “giant bluefin” (size >140 kg in weight or 205 cm curved fork length, CFL) captured by rod and reel in September and October in the southern Gulf of Maine in the northwest Atlantic Ocean and were programmed to release and transmit after 1, 2, 3, or 4 quarters of a year at liberty. These tags did not have pressure sensors or fail-safe mechanisms (see below). Consequently, there is some uncertainty that all data transmitted by the tag were recorded while the tag was actually attached to the fish.

In 2002, the tags were equipped with depth sensors and attached to the dorsal musculature of the fish with flat metal darts constructed of both stainless steel and titanium (Wildlife Computers Inc., Redmond, Washington, USA). The 2002 MWT tag software incorporated a fail-safe mechanism that initiated release and data transmission if the tag approached its depth limit (~1200 m) or remained at a constant depth for 4 days (i.e., if the fish was dead on the bottom or the tag had prematurely detached and was floating at the surface). Most tags were deployed after capture via purse seiner in the southern Gulf of Maine (one was deployed off North Carolina). Groups of up to 20 fish from the same school were captured and released (Wilson et al. 2005). Most in the 2002 deployments were in the commercial category “large medium” (105 kg < weight < 140 kg; 185 cm < CFL < 205 cm) fish. Tags were all programmed to detach from the fish and initiate data transmission on 1 June 2003. In addition to the usual light and temperature sensors, these tags were also equipped with pressure sensors. Details of all tag deployments are given in Table 1.

Times of sunrise and sunset are used to estimate geographic position for each day of transmitted data using the MWT proprietary algorithm. Geographic positions are not estimated for every day at liberty because either no data are received for that day or the light record is not informative of geographic position. We define “reporting rate” for position, temperature, and depth as the proportion of days at liberty with position estimates, temperature records, and

Table 1. Summary of release and reporting information for all tags.

					Position		Depth		Temperature	
Tag No.	Release date	Report date	Weight at release (kg)	Days at liberty	Days	%	Days	%	Days	%
1999–2000 deployment										
2966	24 Sept. 1999	30 June 2000	260.5	281	192	68.3	—	—	—	—
X5312	24 Sept. 1999	30 June 2000	135.9	281	178	63.4	—	—	—	—
3631	25 Sept. 1999	14 Apr. 2000	362.4	203	68	33.5	—	—	—	—
3652	27 Sept. 1999	14 Apr. 2000	226.5	201	133	66.2	—	—	—	—
2975	2 Oct. 1999	14 Sept. 2000		349	169	48.4	—	—	—	—
2974	3 Oct. 1999	14 Sept. 2000	317.1	348	79	22.7	—	—	—	—
X5325	8 Oct. 1999	25 Dec. 1999	158.6	79	62	78.5	—	—	—	—
2979	8 Oct. 1999	25 Dec. 1999	181.2	79	51	64.6	—	—	—	—
3656	8 Oct. 1999	14 Apr. 2000	226.5	190	150	79.0	—	—	—	—
5328	8 Oct. 1999	14 Apr. 2000	181.2	190	123	64.7	—	—	—	—
2982	8 Oct. 1999	31 Aug. 2000	203.9	329	161	48.9	—	—	—	—
3704	8 Oct. 1999	31 Aug. 2000	158.6	329	153	46.5	—	—	—	—
3648	14 Sept. 2000	1 Sept. 2001	181.0	353	129	36.5	—	—	—	—
3665	14 Sept. 2000	1 Sept. 2001	249.2	353	74	21.0	—	—	—	—
3667	14 Sept. 2000	1 Sept. 2001	215.2	353	93	26.4	—	—	—	—
2002 deployment										
4659	17 July 2002	27 July 2002	181.4	11	6	54.6	6	54.6	6	54.6
5026	17 July 2002	29 July 2002	181.4	13	11	84.6	13	100.0	13	100.0
A188	17 July 2002	4 Aug. 2002	136.1	19	9	47.4	10	52.6	10	52.6
5028	17 July 2002	16 Sept. 2002	158.7	62	18	29.0	60	96.8	61	98.4
A191	17 July 2002	18 Sept. 2002	204.1	64	8	12.5	31	48.4	32	50.0
A202	17 July 2002	18 Sept. 2002	204.1	64	20	31.3	33	51.6	33	51.6
A189	17 July 2002	22 Jan. 2003	136.1	190	2	1.1	13	6.8	18	9.5
5027	17 July 2002	20 Feb. 2003	136.1	219	39	17.8	114	52.1	101	46.1
5024	17 July 2002	17 Mar. 2003	113.4	244	68	27.9	120	49.2	113	46.3
5025	17 July 2002	18 Mar. 2003	136.1	245	78	31.8	118	48.2	112	45.7
5280	1 Aug. 2002	15 Sept. 2002	136.1	46	18	39.1	46	100.0	46	100.0
A208	1 Aug. 2002	5 Oct. 2002	136.1	66	4	6.1	2	3.0	7	10.6
A199	1 Aug. 2002	19 Oct. 2002	113.4	80	20	25.0	36	45.0	35	43.8
A205	1 Aug. 2002	29 Oct. 2002	113.4	90	17	18.9	42	46.7	43	47.8
5283	1 Aug. 2002	6 Nov. 2002	90.7	98	32	32.7	92	93.9	93	94.9
5269	1 Aug. 2002	27 Nov. 2002	136.1	119	37	31.1	98	82.4	103	86.6
5267	1 Aug. 2002	9 Dec. 2002	136.1	131	45	34.4	109	83.2	115	87.8
5279	1 Aug. 2002	13 Dec. 2002	181.4	135	19	14.1	95	70.4	90	66.7
A206	1 Aug. 2002	14 Dec. 2002	181.4	136	19	14.0	2	1.5	4	2.9
A190	1 Aug. 2002	29 Dec. 2002	181.4	151	26	17.2	59	39.1	60	39.7
5281	1 Aug. 2002	2 Jan. 2003	90.7	155	30	19.4	130	83.9	129	83.2
5282	1 Aug. 2002	22 Jan. 2003	204.1	175	56	32.0	131	74.9	128	73.1
5272	1 Aug. 2002	25 Jan. 2003	136.1	178	54	30.3	121	68.0	123	69.1
A195	1 Aug. 2002	30 Jan. 2003	136.1	183	37	20.2	17	9.3	17	9.3
5274	1 Aug. 2002	7 Feb. 2003	181.4	191	44	23.0	109	57.1	108	56.5
5271	1 Aug. 2002	20 Feb. 2003	136.1	204	66	32.4	135	66.2	114	55.9
5276	1 Aug. 2002	7 Mar. 2003	158.7	219	51	23.3	107	48.9	116	53.0
5273	1 Aug. 2002	7 Apr. 2003	181.4	250	84	33.6	70	28.0	90	36.0
5270	1 Aug. 2002	7 May 2003	136.1	280	78	27.9	89	31.8	92	32.9
5275	1 Aug. 2002	1 June 2003	181.4	305	107	35.1	133	43.6	125	41.0
5278	1 Aug. 2002	1 June 2003	158.7	305	69	22.6	130	42.6	152	49.8
5362	9 Aug. 2002	18 Aug. 2002	158.7	10	10	100.0	10	100.0	10	100.0
5305	9 Aug. 2002	18 Aug. 2002	136.1	10	10	100.0	10	100.0	10	100.0
5302	9 Aug. 2002	21 Aug. 2002	90.7	13	12	92.3	12	92.3	12	92.3
5019	9 Aug. 2002	31 Aug. 2002	136.1	23	19	82.6	23	100.0	23	100.0
5021	9 Aug. 2002	19 Sept. 2002	136.1	42	13	31.0	42	100.0	42	100.0
5020	9 Aug. 2002	24 Sept. 2002	158.7	47	24	51.1	47	100.0	47	100.0

Table 1 (*concluded*).

					Position		Depth		Temperature	
Tag No.	Release date	Report date	Weight at release (kg)	Days at liberty	Days	%	Days	%	Days	%
5314	9 Aug. 2002	26 Oct. 2002	158.7	79	17	21.5	74	93.7	76	96.2
5320	9 Aug. 2002	4 Nov. 2002	136.1	88	30	34.1	83	94.3	84	95.5
5374	9 Aug. 2002	11 Dec. 2002	136.1	125	35	28.0	110	88.0	110	88.0
5023	9 Aug. 2002	15 Dec. 2002	158.7	129	52	40.3	108	83.7	102	79.1
5310	9 Aug. 2002	19 Dec. 2002	147.4	133	38	28.6	81	60.9	81	60.9
5376	9 Aug. 2002	16 Feb. 2003	136.1	192	45	23.4	126	65.6	125	65.1
5301	9 Aug. 2002	22 Feb. 2003	136.1	198	43	21.7	98	49.5	104	52.5
5268	9 Aug. 2002	7 Mar. 2003	90.7	211	40	19.0	116	55.0	108	51.2
5367	9 Aug. 2002	1 June 2003	113.4	297	39	13.1	181	60.9	173	58.3
5303	17 Aug. 2002	1 Mar. 2003	113.4	197	34	17.3	56	28.4	55	27.9
X5325	6 Sept. 2002	25 Sept. 2002	204.1	20	3	15.0	20	100.0	20	100.0
X5312	30 Sept. 2002	6 Oct. 2002	226.8	7	2	28.6	7	100.0	7	100.0
5365	30 Sept. 2002	6 Oct. 2002	249.4	7	5	71.4	7	100.0	7	100.0
5377	30 Sept. 2002	8 Oct. 2002	181.4	9	3	33.3	9	100.0	9	100.0
5313	30 Sept. 2002	12 Oct. 2002	294.8	13	2	15.4	13	100.0	13	100.0
5307	30 Sept. 2002	16 Oct. 2002	272.1	17	5	29.4	17	100.0	17	100.0
5352	30 Sept. 2002	24 Oct. 2002	204.1	25	3	12.0	25	100.0	25	100.0
5299	30 Sept. 2002	1 Nov. 2002	204.1	33	9	27.3	33	100.0	33	100.0
5369	30 Sept. 2002	1 Feb. 2003	226.8	125	17	13.6	74	59.2	73	58.4
5265	10 Oct. 2002	16 Oct. 2002	181.4	7	3	42.9	7	100.0	7	100.0
5328	10 Oct. 2002	9 Nov. 2002	272.1	31	17	54.8	31	100.0	31	100.0
5326	14 Jan. 2003	11 May 2003	124.7	118	65	55.1	99	83.9	98	83.1
Median (1999 releases)			203.9	242	142	64.0	—	—	—	—
Median (2000 releases)			215.2	353	93	26.4	—	—	—	—
Median (2002 releases)			147.4	118	20	28.6	59	70.4	60	69.1

Note: Days at liberty is the number of days between the dates of release and reporting. The columns of Position, Depth, and Temperature report the number of days and the percentage of days at liberty with position, depth, and temperature estimates, respectively. No data were available for Depth and Temperature for releases in 1999 and 2000.

depth records, respectively. MWT PSATs broadcast estimate time of sunrise and sunset and temperature records covering 1 day in a single transmission to the tag manufacturer via the Argos satellite network. For tags with pressure sensors, the pressure records for the day are broadcast in a second transmission (P.W. Howey, Microwave Telemetry Inc., Columbia, Maryland, USA, personal communication). Since there is a only a small number of transmission windows available on any given day, tags which broadcast pressure records report only 50% as many sunrise and sunset records during a day as tags that do not broadcast pressure records. As a result, the position reporting rate for pressure-recording tags will be lower than that of tags that only transmit sunrise and sunset records.

The sequence of geographic positions estimated by the MWT geolocation tracks were analyzed using several variants of a state–space model estimated by the extended Kalman filter. Strictly speaking, the Kalman filter is a likelihood method that is applied to estimate the parameters of a state–space model. The term Kalman filter is often used to refer to the combined state–space and likelihood models. For simplicity, we will refer to the state–space model estimated by the extended Kalman filter as the Kalman filter or KF. The KF and the several variants used in this paper are described in the supplementary material[2] and Nielsen (2004). The model parameterizes movement as a biased random walk partitioning movement into directed movement (i.e., the eastward (u) and northward (v) bias of the random walk) and dispersive movement (i.e., random variation in movement, D). The KF also estimates the in situ geolocation errors as the longitude (σ_x) and average latitude (σ_{y_0}) standard deviations. The equinox singularity model (Sibert et al. 2003) was used to estimate latitude geolocation errors. This parameterization enables estimation of latitude during the several days surrounding the equinox, when latitude as a function of day length is indeterminate. Two additional parameters are estimated: the maximum equinox error adjustment (a_0) and the number of days that the maximum equinox error is shifted towards the boreal summer solstice (b_0) (Hill and Braun 2001).

The first two model variants pertain to whether movement is assumed to be homogeneous during the entire time at liberty. The “change-point” model (Nielsen 2004) treats the track as a sequence of two distinct behaviors: an early and a

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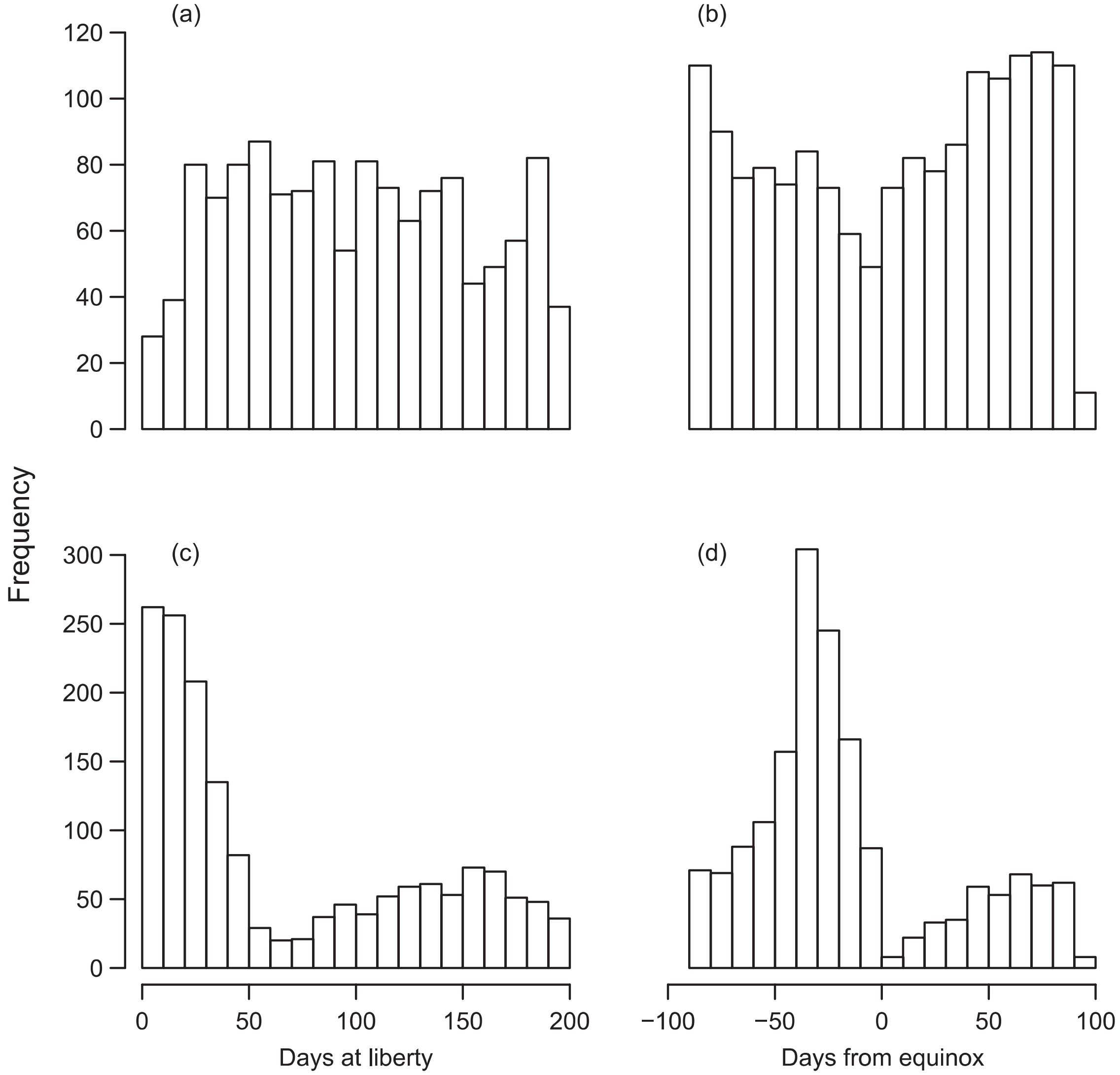
[2] Supplementary data for this article are available on the journal Web site (http://cjfas.nrc.ca) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 5074. For more information on obtaining material refer to http://cisti-icist.nrc-cnrc.gc.ca/irm/unpub_e.shtml.

Fig. 1. Temporal distribution of position estimates for the combined 1999 and 2000 (*a*, *b*) and the 2002 (*c*, *d*) deployments. Frequency of position estimates by 10-day period during the first 200 days liberty are shown in panels *a* and *c*. Frequency of position estimates by 10-day period in relation to the equinoxes are shown in panels *b* and *d*. Negative days indicate days prior to the equinox; positive days indicate days after the equinox. For longer periods at liberty, the histograms include observations relative to both equinoxes.



later period. The change point (i.e., the exact time when the behavior switches (τ)) is estimated by maximum likelihood. The change-point track is represented by 11 parameters: three movement parameters for each segment (u_1, v_1, D_1; and u_2, v_2, D_2), the change point (τ), and four error parameters (σ_x, σ_{y_0}, a_0, and b_0). The multisegment KF variant accommodates variation in behavior by estimating different values of the movement parameters in different arbitrary geographic areas. The third KF variant pertains to whether the tracks are treated as unique events or as samples from a population. A single track model assumes that each track is unique and has distinct parameters for each track. The multitrack KF model assumes that tracks are samples from a population and represents all tracks by a single (small) set of parameters.

The state–space model represents movement as a biased random walk, the Lagrangian analog of the advection diffusion model applied to tagged tuna by Sibert et al. (1999). The biased random walk model is also the basis of the model used by Humston et al. (2000) to simulate attraction of bluefin tuna to temperature fronts. The model parameters estimated by the KF can be applied in either an advection–diffusion model or in a biased random walk. We apply a biased random walk to simulate movements of individual tagged fish to project their movements beyond the tag shedding dates. The simulated release position was near 68°W by 41°N, near the actual release positions off Cape Cod in the northwest Atlantic. The movement parameters were those estimated from the 1999 and 2002 deployments by the two-region, multitrack model. The movements of populations of 100 tagged fish were simulated for 360 days, and their positions were reported after 30, 90, and 360 days at liberty.

All variants of the KF were implemented in AD Model Builder (Otter Research Ltd. 1994–1999). Model parameters were estimated by numerical minimization of the extended KF likelihood function either by a quasi-Newton function minimizer or by Markov chain Monte Carlo (MCMC) optimization (Geyer 1996; Gelman et al. 2004).

Results

Details of the deployment and reporting are presented in Table 1. The earliest reporting tags (X5325 and 2979; 25 December 1999) were the first PSAT reports from deployments on a marine vertebrate. Fish tagged in 1999 and 2000 (>200 kg) were substantially larger than those tagged in 2002 (<150 kg) because almost all fish in 2002 were tagged and released from a commercial purse seiner that primarily captured large medium fish during the 2002 season. The median number of days at liberty for the 1999, 2000, and 2002 deployments were 242, 352, and 118 days, respectively, reflecting differences in programmed reporting date. The number of days with position estimates were 142, 93, and 20, respectively. Approximately 64% of the days at liberty for 1999 tags had position estimates compared with 26% to 29% for the 2000 and 2002 tags. The temperature and depth reporting rates for the 2002 tags were both approximately 70%, about twice the position reporting rate.

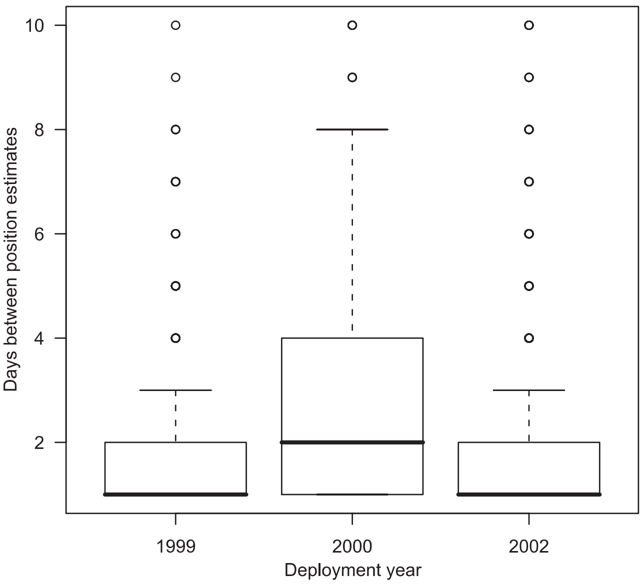
The distribution of position estimates over the days at liberty was not uniform (Fig. 1). The rate of recovery of position estimates was lowest around the time of the equinoxes for both tag groups. All of the 1999 and 2000 tags were released within 2 weeks of 21 September, the height of the New England bluefin fishing season and the approximate date of the boreal autumnal equinox. The position recovery rate was low for these tags during the first month at liberty and relatively constant thereafter. Most of the 2002 releases were in July and August, well before the equinox, and the position recovery rate was high during the first month at liberty. The tags deployed in September and October 2002 were at liberty for relatively short periods and had low rates of position reporting.

Substantial gaps occur in the time series of position estimates. The time interval between successive geolocation estimates (Δt) ranges from 1 to 120 days, the maximum gap recorded in the 2002 deployments. The 1999 and 2002 deployments are similar, with 50% of the observations separated by gaps of 1 and 2 days (Fig. 2). The observations from the 2000 deployment are more dispersed, with 50% of the observations separated by gaps of 1–4 days and a large number of gaps of more than 4 days.

The change-point variant of the KF requires 11 parameters; therefore, only tracks with 20 or more data points were analyzed (Table 2). The median estimated longitude geolocation errors, σ_x, ranges from 0.35° for the 2000 deployments to 0.93° for the 2002 deployments. The median estimated latitude geolocation error, σ_{y_0}, ranges from 1.03° for the 1999 deployments to 2.11° for the 2002 deployments. The parameters of the equinox singularity latitude error correction are not well-determined by the data, especially for the 2002 tags. The timing parameter, b_0, is in some cases on its upper bound of 50 days. Consequently, extremely large values of σ_{y_0} are estimated for some of the 2002 tags.

The two-segment change-point model provides a significantly better description of the data at the 95% confidence level than the one-segment model for nearly all tracks, as determined by likelihood ratio tests (Table 3). Estimates of the directed movement parameters, u and v, are near zero for both segments of most tracks. Estimates of nondirected movement parameters, D, are highly variable. All of the reporting positions and most of estimated change-point positions for the 1999 and 2000 deployments occurred in the North Atlantic Subtropical Gyre (NAST) biogeochemical province (Longhurst 1998). The reporting positions and estimated change-point provisions for the 2002 deployments occurred closer in shore, usually within Northwest Atlantic Shelves (NWCS) province (Fig. 3). The distribution of the estimated change points for the 1999 deployment is very similar to the time to shedding recorded by the tags for the 2002 deployment (Fig. 4). The median days at liberty to the estimated 1999 change point is 122 compared with the 118 days for the median days to shedding for the 2002 deployments.

Fig. 2. Frequency distribution of time intervals between geolocation estimates (Δt) for the 1999, 2000, and 2002 deployments. The boxes indicate the interquartile range (i.e., the area encompassing the central 50% of the time intervals). The horizontal line within the box indicates the median. The range bars extend outside the boxes to the most extreme data point, which is no more than 1.5 times the interquartile range. The circles are individual outliers. The ordinate has been truncated at 10 days.



The data from the three deployments were analyzed by the multitrack Kalman with two regions separated by the approximate boundary between the NWCS and Gulf Steam (GFST) provinces. Tracks from the 1999 and 2000 deployments were truncated on the day closest to the estimated change point and the positions of the change points assumed to be “known” reporting positions (i.e., fixed endpoints) in the KF analysis (Table 4).

The geolocation errors estimated by the combined multitrack model were slightly higher than medians of the estimates from the single-track models (Table 2). Estimated values of the dispersive movement parameter (D) for the multitrack models were higher than the median estimates from single-track models, and the absolute values of directed movement parameters (u, v) were also higher than for the single-track models.

Table 2. Summary of parameter estimates for all tags using the change-point variant of the Kalman filter model.

Tag	u_1	v_1	D_1	u_2	v_2	D_2	σ_x	σ_{y_0}	a_0	b_0
2966*	7.79	1.00	535.6	0.78	–3.60	175.5	0.38	0.91	0.0427	20.26
X5312*	—	—	363.3	—	—	4.3	0.44	1.46	0.0055	11.69
3631*	19.75	–1.79	1997.6	6.22	5.93	317.7	0.37	1.11	0.0651	17.07
3652*	—	—	1061.4	—	—	163.2	0.45	1.07	0.0154	14.69
2974*	7.16	–0.62	680.4	3.71	0.48	89.0	0.54	0.89	0.0198	14.58
2975*	6.91	–3.41	542.9	0.32	1.81	115.5	0.44	0.92	0.0314	24.95
X5325*	—	—	1755.1	—	—	584.2	0.45	0.68	0.0202	37.39
2979*	—	—	1837.2	—	—	330.4	0.00	1.12	0.1534	–50.00
3656*	4.01	–1.69	870.4	5.05	–7.73	137.1	0.22	1.35	0.0563	13.85
5328*	23.11	–2.78	1656.9	3.33	–1.59	266.9	0.29	1.13	0.0369	13.02
2982*	3.84	–4.51	3117.8	5.29	0.08	288.6	0.50	0.84	0.0131	12.20
3704*	—	—	665.5	—	—	130.0	0.36	1.00	0.0277	16.25
3648*	—	—	540.9	—	—	155.4	0.29	1.37	0.0000	–0.04
3665*	—	—	457.4	—	—	158.5	0.35	2.62	0.0003	–1.07
3667*	—	—	2777.1	—	—	138.0	0.49	2.09	0.0001	–0.76
5374*	—	—	1983.4	—	—	301.9	0.00	1.56	0.9614	0.90
5303*	—	—	67.1	—	—	5208.7	1.40	1.65	0.0000	–1.02
5326*	—	—	11.3	—	—	2216.1	0.90	2.49	0.2163	–3.85
5376	—	—	1174.5	—	—	212.1	0.40	2.23	0.5548	23.29
A195*	—	—	2.1	—	—	254.2	0.69	1.11	0.1060	–10.68
5023*	—	—	2786.3	—	—	132.0	0.22	1.31	0.2151	–37.32
5024*	—	—	8.7	—	—	780.3	1.07	1.72	0.4363	20.27
A199	—	—	641.7	—	—	123.0	0.92	2.43	0.1304	50.00
5025*	—	—	151.1	—	—	6.6	0.95	2.10	0.3086	43.40
A202*	—	—	946.5	—	—	9.0	0.00	0.26	0.0047	–8.59
5367	—	—	516.9	—	—	1397.1	0.98	2.86	1.5738	50.00
5027*	—	—	81.8	—	—	1274.5	1.03	2.42	1.7289	–42.86
5301*	—	—	297.9	—	—	4.6	0.84	2.39	0.5868	15.86
5267*	—	—	513.1	—	—	3.5	0.53	2.51	1.5494	50.00
5268*	—	—	3.0	—	—	983.6	0.85	1.56	0.3146	2.52
5269*	—	—	1233.3	—	—	106.6	0.53	1.22	0.0000	28.84
5270	—	—	323.3	—	—	94.4	0.93	3.36	2.2457	50.00
5271*	—	—	4263.1	—	—	318.3	1.42	2.70	0.5467	8.43
5272*	—	—	204.4	—	—	2231.7	0.89	0.71	0.0663	–29.81
5273*	—	—	159.3	—	—	1032.1	1.12	2.05	0.2941	22.71
5274	—	—	599.3	—	—	227.1	0.78	0.91	0.1472	–5.79
5275*	—	—	291.0	—	—	1788.0	1.23	2.26	0.2801	28.50
5276*	—	—	50.5	—	—	2329.1	1.01	15.00	32.1238	–50.00
5281	—	—	47.6	—	—	418.4	1.11	2.13	0.5864	50.00
5282	—	—	24.0	—	—	316.5	1.40	12.52	23.7936	49.99
5283*	—	—	26.6	—	—	1579.1	0.48	1.35	0.0711	8.09
5310*	—	—	5.1	—	—	366.7	1.41	1.08	0.2505	–25.32
5320*	—	—	1658.3	—	—	122.8	1.09	2.58	0.9150	50.00
Median 1999	3.92	–0.31	965.9	0.55	0.00	169.4	0.41	1.03	0.0296	14.64
Median 2000	0.00	0.00	540.9	0.00	0.00	155.4	0.35	2.09	0.0001	–0.76
Median 2002	0.00	0.00	247.7	0.00	0.00	317.4	0.93	2.11	0.0312	12.14

Note: An asterisk (*) after a tag number indicates that division of the track into two segments is statistically significant ($P < 0.05$). A dash (—) indicates parameters were not significantly different from zero. (Estimates of the change points are listed in Table 3.)

Larger data sets were constructed by combining tracks from the three deployments. The significance of the difference between the 1999 and 2002 tracks was evaluated by a likelihood ratio test comparing the combined data with the aggregated results for the 1999 and 2002 tracks. The fit to the combined data produced a log likelihood of –8946.57 with 10 parameters, and the aggregate model had a higher likelihood of –8501.06 (2825.38 + 5675.68) with 20 parameters (Table 4). The resulting χ^2 statistic was 891.02 with 10 degrees of freedom, significant at $P < 0.001$. The aggregate model consisting of two 10-parameter models was significantly more consistent with the combined 1999–2002 data than a single 10-parameter model. That is, the movements recorded by the 1999 and 2002 deployments were significantly different.

This result is not surprising, since the parameters estimated from these two data sets differ in almost all respects. The geolocation errors are higher for the 2002 deployments than for the 1999 deployments. The estimates of both dispersive and directed movement parameters are higher for the 1999 deployment. The directions of movement, particularly in the offshore area, also differ. The movement of tags from the 1999 deployment show a strong easterly orientation (H_2 = 92°) compared with a northwest orientation for the 2002 deployment (H_2 = 319°).

The positions of 100 simulated tagged fish after different periods at liberty (Fig. 5) using the movement parameters estimated from the 1999 and 2002 deployments are shown in Table 4. These two sets of movement parameters produce very different tag distributions over time. The distribution predicted from the 1999 estimated movement pattern covers most of the North Atlantic Ocean, with nearly all tags crossing the 45°W stock separation line in less than 12 months. In contrast, the distribution predicted from the estimated 2002 movement pattern is largely confined to the western North Atlantic, with no tags crossing 45°W longitude.

Discussion

Estimation of latitude from light data is nearly impossible during the time period surrounding the equinox because day length is nearly the same at all latitudes. The equinox latitude error model in the KF compensates for this problem by amplifying the error in latitude estimation during equinox periods. The reporting rate of geolocation estimates from PSATs is lowest around the equinoxes and generally less than 50%. When field operations require release of tagged fish at times of year when PSAT data yield few position estimates, the resulting data will be a biased sample of the movement pattern. For example, tags released within 2 weeks of the equinox will not sample the behavior of the animal during its first months at liberty. The 2002 release strategy effectively improved reporting during the first part of the track by releasing more tags earlier in the year during periods not affected by the equinox. Use of multisegment movement models can alleviate this problem by estimating separate parameters for the first and and last part of the track. The multitrack model may further improve coverage of geographically variable behavior by distributing observations more evenly among regions.

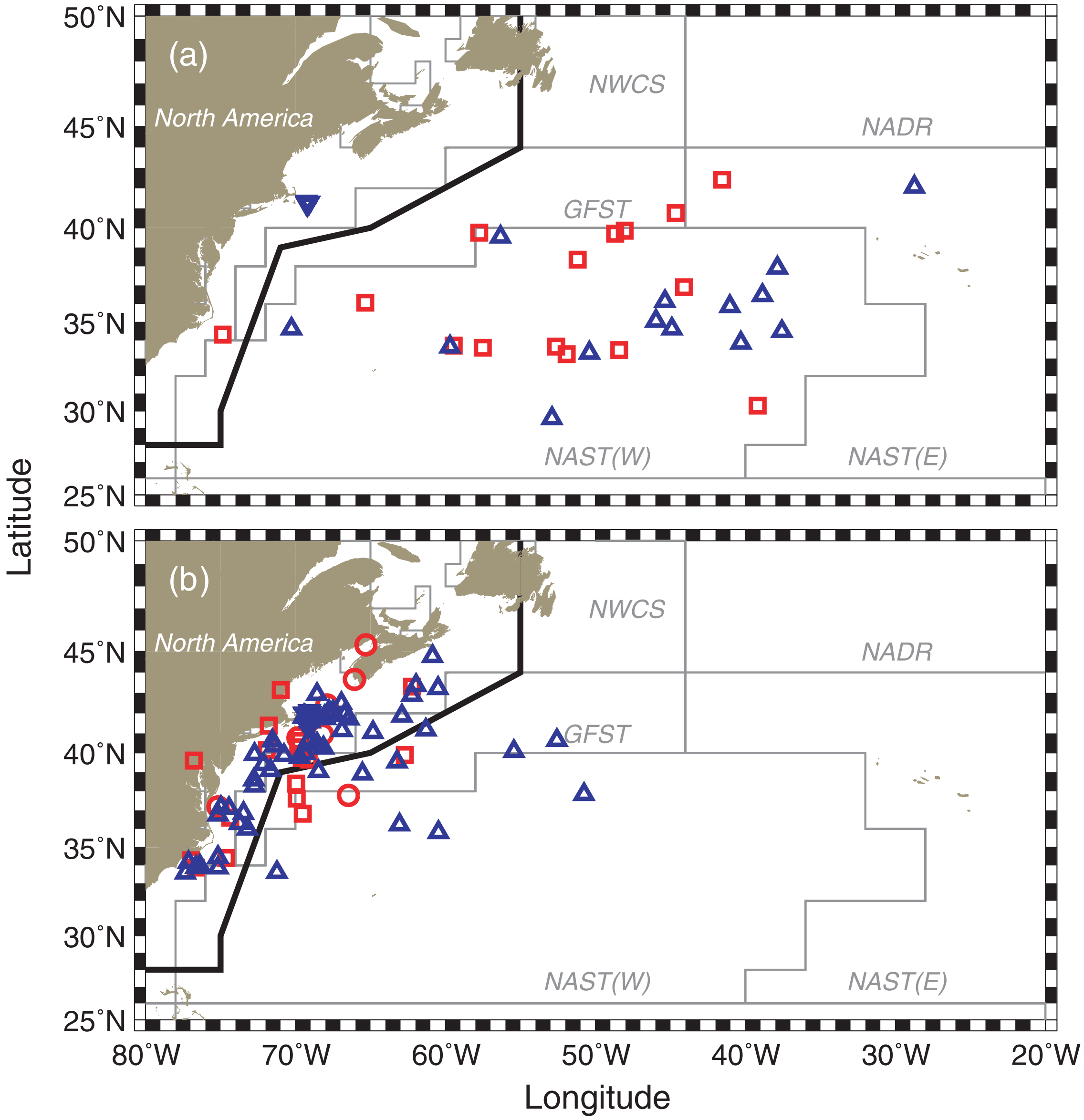
The inherent limits of light-based algorithms at the equinox do not entirely account for low position reporting rates in the 2000 and 2002 data. Transmission to Argos satellites is constrained to approximately 10 transmission windows per day (P.W. Howey, Microwave Telemetry Inc., Columbia, Maryland, USA, personal communication). The 1999 tags were transmitting only light and temperature data and were able to transmit a complete daily record in one transmission. The 2000 and 2002 tags were also transmitting depth data and therefore required two transmissions for a complete daily record. These difference could explain the roughly twofold change in position reporting rate. There are multiday gaps in all tracks at times of year other than around the equinox. The loss of 1 day of transmission from the 1999 tags could cause a 10-day gap in the track, and loss of 1 day of transmission from the 2000 and 2002 tags would cause a roughly 5-day gap. Whether these gaps are due to weather or to localized interference with transmission from the tag to the

Table 3. Summary of Kalman filter change-point estimates of all tags.

Tag	τ	Date	P	Longitude (°E)	Latitude (°N)
2966	153	24 Feb. 2000	0.0010	318.43	42.42
X5312	252	2 June 2000	0.0001	300.55	33.71
3631	49	13 Nov. 1999	<0.0001	311.93	39.86
3652	136	10 Feb. 2000	<0.0001	315.91	36.89
2974	153	4 Mar. 2000	0.0001	315.35	40.75
2975	203	22 Apr. 2000	<0.0001	320.82	30.29
X5325	33	10 Nov. 1999	0.0315	285.13	34.31
2979	71	18 Dec. 1999	0.0124	302.25	39.76
3656	137	22 Feb. 2000	<0.0001	302.49	33.58
5328	42	19 Nov. 1999	<0.0001	308.80	38.35
2982	86	2 Jan. 2000	<0.0001	294.63	36.05
3704	206	1 May 2000	<0.0001	308.09	33.21
3648	209	11 Apr. 2001	0.0002	307.36	33.63
3665	204	6 Apr. 2001	0.0164	311.57	33.44
3667	90	13 Dec. 2000	<0.0001	311.31	39.70
5374	19	27 Aug. 2002	0.0006	290.29	40.60
5303	132	27 Dec. 2002	<0.0001	289.02	43.15
5326	84	8 Apr. 2003	0.0002	285.37	34.39
5376	20	28 Aug. 2002	0.0801	293.53	37.78
A195	40	10 Sept. 2002	0.0184	290.78	41.97
5023	50	27 Sept. 2002	<0.0001	290.08	37.61
5024	30	16 Aug. 2002	0.0007	290.95	41.99
A199	11	12 Aug. 2002	0.2444	290.17	40.77
5025	156	20 Dec. 2002	0.0092	285.65	36.60
A202	41	27 Aug. 2002	<0.0001	290.18	40.29
5367	19	27 Aug. 2002	0.1706	293.92	43.67
5027	138	2 Dec. 2002	0.0012	288.08	40.13
5301	162	17 Jan. 2003	0.0189	297.77	43.31
5267	112	21 Nov. 2002	0.0074	283.01	34.29
5268	32	9 Sept. 2002	0.0001	290.82	41.86
5269	39	9 Sept. 2002	0.0264	290.46	36.82
5270	107	16 Nov. 2002	0.1162	284.83	37.17
5271	14	15 Aug. 2002	0.0052	290.40	39.74
5272	169	17 Jan. 2003	0.0055	297.27	39.89
5273	206	23 Feb. 2003	0.0396	283.34	33.86
5274	106	15 Nov. 2002	0.1722	294.69	45.31
5275	199	16 Feb. 2003	0.0082	283.20	39.59
5276	162	10 Jan. 2003	<0.0001	290.86	39.66
5281	115	24 Nov. 2002	0.0797	291.80	40.94
5282	125	4 Dec. 2002	0.1632	292.09	42.43
5283	29	30 Aug. 2002	0.0062	288.20	41.37
5310	13	21 Aug. 2002	0.0475	291.03	41.90
5320	9	17 Aug. 2002	0.0119	290.05	38.40

Note: τ is the estimated day at liberty estimated for the change point; Date is the estimated date of the change; P is the signicance level of the improvement in fit of the two-segment model over the one-segment model; and Longitude and Latitude are the estimated position of the change.

Fig. 3. Reporting and estimated change-point locations for pop-up satellite archival tags (PSATs) released in 1999 and 2000 (*a*) and in 2002 (*b*). Reporting points are given by triangles (△). Change points for $P \leq 0.05$ are plotted with open squares (□); change points for $P > 0.05$ are plotted with open circles (○). The inverted triangles (▽) indicate release position. The heavy black line indicates the boundary between the regions used in the two-segment multitrack analyses. The gray lines indicate the boundaries of the Longhurst (1998) biogeographic provinces in the Northwest Atlantic. NWCS, Northwest Atlantic Shelves; NADR, North Atlantic Drift; GFST, Gulf Steam; NAST, North Atlantic Subtropical Gyre.



satellite is unknown. However, examination of available weather and wave height records during the deployments cannot simply account for the observed transmission gaps.

Wilson et al. (2005) found no evidence of movement east of 45°W longitude based on the positions reported for the 2002 deployment through 1 June 2003. Simulations based on the same data are consistent with this conclusion. The most important difference between the two deployments is between the estimated movement direction in the offshore region. The estimated heading for the 2002 deployments is 319°, a heading that would return a fish to coastal waters if it had moved into the offshore area. In contrast, the estimated heading in the offshore area for the 1999 deployment is 92°, a heading that would start a fish on a transatlantic migration.

Changes in oceanographic conditions such as thermocline depth and sea surface temperature fronts occurred over the tagging periods (M.E. Lutcavage, unpublished data), and shifts in availability of surface schools were reflected in declines in catch per unit of effort (CPUE) for harpoon and purse seine fisheries. PSAT data also recorded shifts in modal depth preferences for bluefin tuna, with fish in 2002 remaining somewhat deeper than fish tagged in 1999–2001 (Wilson et al. 2005).

The result of the two-segment multitrack analysis of the 1999–2001 data is consistent with the hypothesis that bluefin

Table 4. Results of multitrack Kalman filter analyses for the 1999, 2000, and 2002 deployments.

(*a*) The negative log-likelihood value, number of parameters, and estimates of geolocation errors.

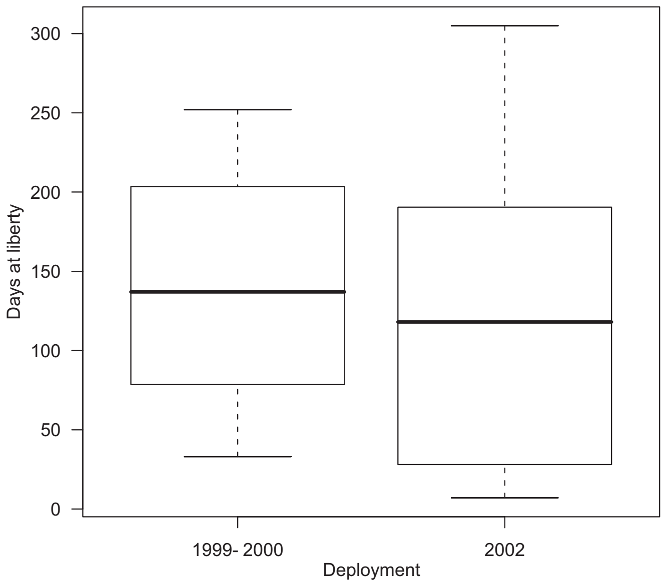
Year	Tracks	$-\log L$	n	σ_x	σ_y	σ_{xy}	a_0	b_0
1999	12	2825.38	10	0.38	1.20	1.26	0.00585	14.07
2000	3	787.836	10	0.43	2.48	2.51	0.00047	−0.60
2002	28	5675.68	10	1.07	2.36	2.59	0.54144	20.25
1999+2002	40	8946.57	10	0.85	1.51	1.73	0.04658	14.25
Aggregate	40	8501.06	20					

(*b*) Estimates of movement parameters for the inshore and offshore regions.

		Inshore						Offshore					
Year	Tracks	T_1	u_1	v_1	D_1	S_1	H_1	T_2	u_2	v_2	D_2	S_2	H_2
1999	12	149	2.86	−14.00	1221.3	14.29	168.4	588	7.29	−0.28	812.6	7.30	92.2
2000	3	47	5.61	3.00	1984.3	6.36	61.9	119	3.70	−1.46	317.8	3.98	111.5
2002	28	1139	1.04	−1.33	334.8	1.69	142.1	228	−1.20	1.39	685.8	1.83	319.2
1999+2002	40	1280	1.21	−2.11	486.0	2.43	150.2	913	3.15	0.11	632.5	3.16	88.0

Note: Tracks refers to the number of tracks included in the model. Aggregate is the aggregated model consisting of the sum of the 1999 and 2002 models.

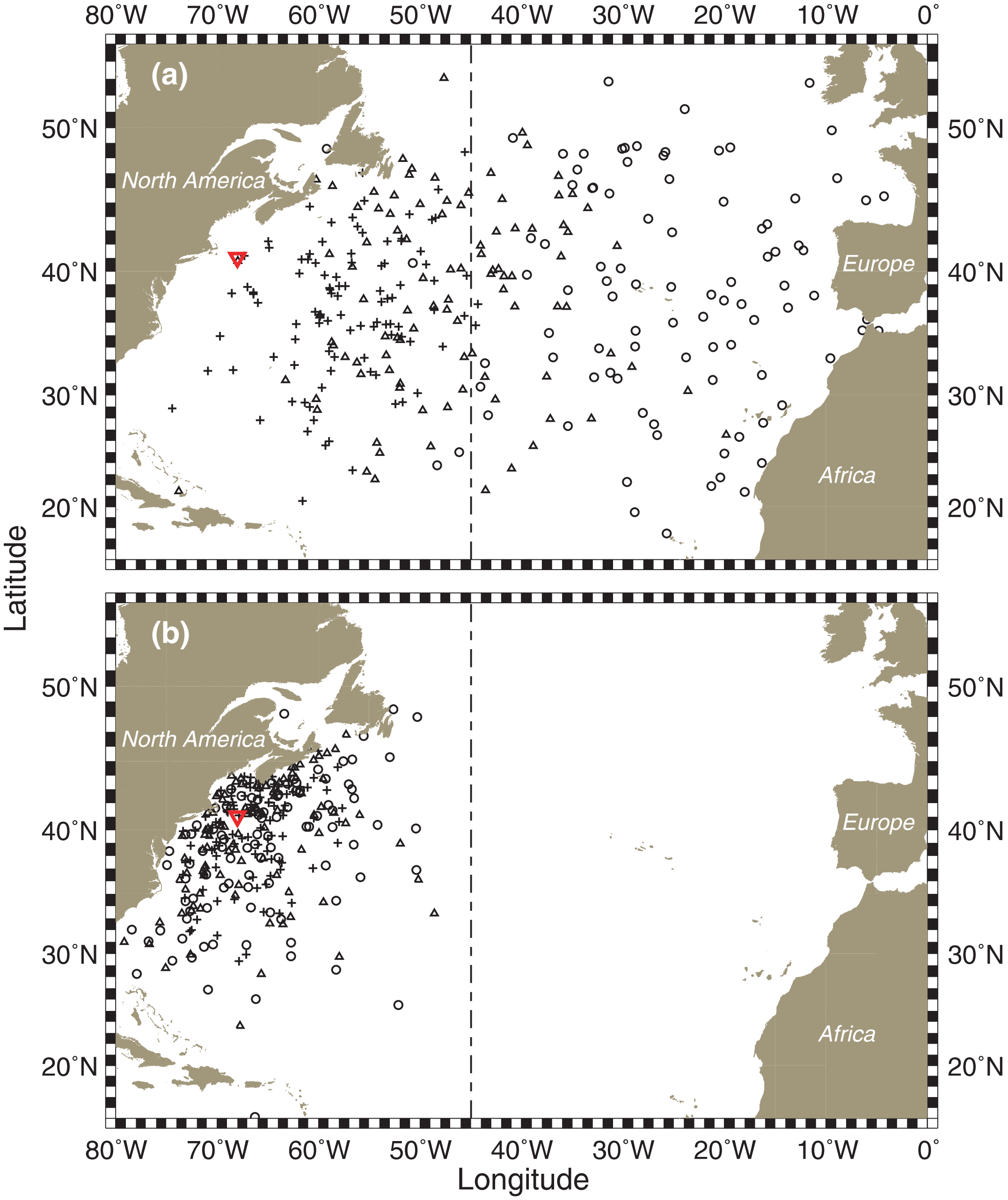
Fig. 4. Days at liberty prior to tag shedding. Data for 1999–2000 illustrates days prior to the estimated change point for the 1999 and 2000 deployments; data for 2002 illustrates days prior to reporting date for 2002 deployments. The boxes indicate the interquartile range (i.e., the area encompassing the central 50% of the time intervals). The horizontal line within the box indicates the median. The range bars extend outside the boxes to the most extreme data point, which is no more than 1.5 times the interquartile range.



tuna change their behavior when they move away from the coast and the NWCS province to begin a transatlantic migration. After leaving the shelf, bluefin feeding dependencies shift from demersal fishes (i.e., Atlantic herring (*Clupea herrengus*), Atlantic mackerel (*Scomber scombrus*), and American sand lance (*Ammodytes americanus*)) to squid, octopods, and mesopelagic fishes (Matthews et al. 1977). Longline catches (Wilson 1965; Shingu et al. 1975) and also PSAT data show that depth associations shift, especially near the Gulf Stream boundary (Wilson et al. 2005).

Differences in apparent behavior recorded by the tags deployed in different years suggest significant interannual variability in the movement and distribution of Atlantic bluefin tuna. Mather (1980) showed that transatlantic migration of large and small bluefin tuna varied strongly from year to year and hypothesized that it might be linked to oceanographic conditions. The fish tagged in 1999 and 2000 were larger than those tagged in 2002, and there were environmental differences between the two periods as well. In 1996, the North Atlantic Oscillation (NAO) index exhibited the largest single-year drop in the 20th century, attaining a negative value not seen since the 1960s, and hydrographic conditions in the mid-Atlantic Bight did not return to their pre-1996 state until the end of 1999 (Smith et al. 2001; Greene and Pershing 2003). These changes had a profound impact on water temperatures (Slonosky and Yiou 2002) and zooplankton communities (Smith et al. 2001) and almost certainly altered the forage base for bluefin tuna. For example, the chlorophyll content in the NWCS during the summer months of 1999 was 25% lower than during the summer months of 2002 (Fig. 6). The 1999 deployment occurred during a pe-

Fig. 5. Simulated positions of 100 tagged fish after 30 days (+), 90 days (△), and 1 year (○) at liberty. Distribution was computed using *u*, *v*, and *D* estimated from the 1999 (*a*) and 2002 (*b*) deployments. The broken line at 45°W longitude is the line used to separate bluefin tuna (*Thunnus thynnus*) stock management units. The inverted triangle (▽) indicates release position.



riod of rapid transition from a negative to a positive phase of the NAO just prior to the end of the recovery period from this major oceanographic change (Fig. 7). Changes in thermal structure and chlorophyll content are not equivalent to changes in tuna forage. Some lapse of time is required for a forage base for top predators to develop from primary productivity (Vinogradov 1981; Jaquet and Whitehead 1996; Gascuel et al. 2005). Lehodey et al. (1998) modeled the forage base for Pacific skipjack tuna (*Katsuwonus pelamis*) using a time lag of 90 days between primary production and forage production. Low productivity from May through July could translate into low forage abundance in September, when the fish tagged in 1999 exited the NWCS province. Our results are consistent with Mather's hypothesis that transatlantic migration is size-dependent and related to environmental conditions in the western Atlantic.

Tag shedding is an chronic problem in the use of pop-up tags (Holland and Braun 2003). The tags used in 2002 were equipped to detect shedding, but that technology was not available in the first generation PSATs used for the 1999 and 2000 deployments. We address the tag shedding problem in data from these tags by attempting to estimate the shedding date and position using the change-point variant of the KF model. The change-point model was able to detect substan-

Fig. 6. Average monthly chlorophyll content of the water in the Northwest Atlantic Shelves province from SeaWiFS data. The horizontal lines indicate the average chlorophyll content in the province for the months of May, June, July, and August. Inverted triangles indicate deployment dates.

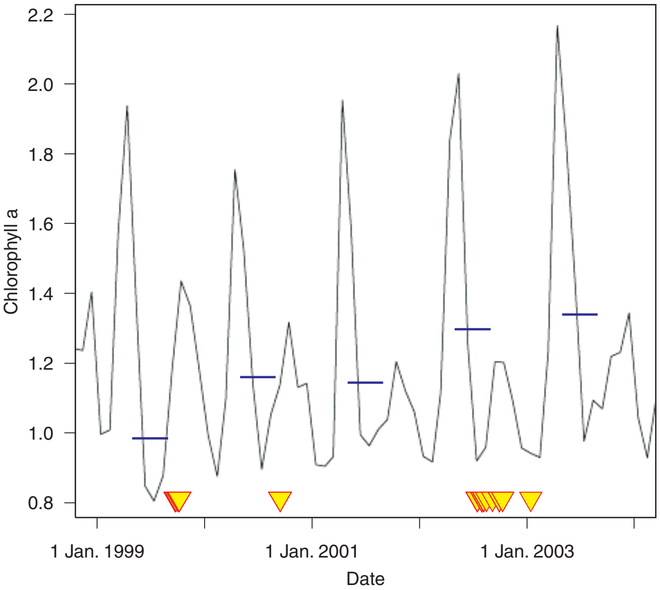
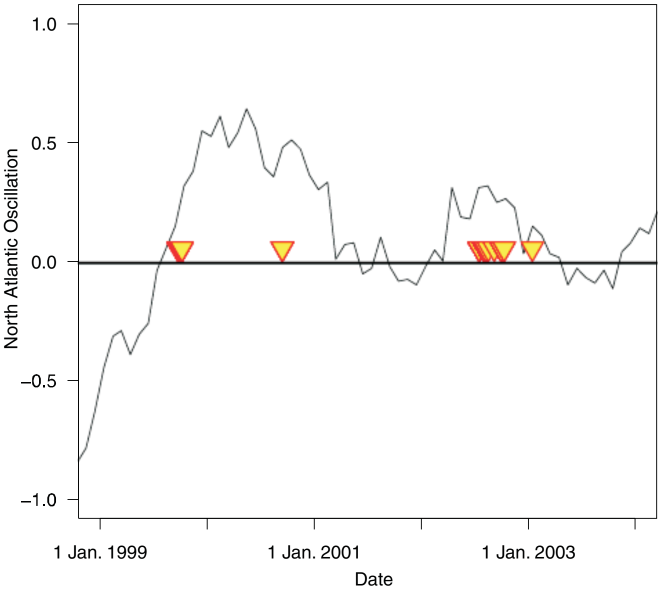


Fig. 7. Twelve-month leading moving average of the North Atlantic Oscillation for 1999 through 2003. Inverted triangles indicate deployment dates. Data are from the National Oceanic and Atmospheric Administration (NOAA) Climate Prediction Center website (http://www.cpc.ncep.noaa.gov/data/teledoc/nao.shtml).



tial differences in apparent movement in two-segment tracks, and the estimated times to shedding are comparable with those recorded by the tags used in the 2002 deployment. Thus we accept the conclusion that the results of the combined 1999 multitrack analysis represent the movement of the bluefin population during the last quarter of 1999. The results of treating the tracks from the two deployment periods as samples of a larger population of tracks using the multitrack model strongly indicate interannual differences in movement.

The joint influence of environment and age on the distribution of bluefin tuna is well known. Mather (1980) indicated that transatlantic mixing could be attributed to both environmental variability and size, and Tiews (1963) attributed eastward movement to the availability of food. Since the fish taggged in 2002 were considerably smaller than those taged in 1999–2000, the results presented here cannot discrimate between envrionment and age. Indeed, it is probably unrealistic to search for a single cause. Regardless of the causes of the interannual variability, the differences have profound fishery management implications, because in some years, most of the population may cross the current stock separation line at 45°W longitude. Other spatially fixed management frameworks, such as those recently proposed by International Commission for the Conservation of Atlantic Tunas (ICCAT 2002), will also be impacted by interannual variability, as noted by Powers and Porch (2004). The possibility of environmental controls mediating the distribution of the stock should be seriously considered by fishery managers when geographically assigning catch quotas or in defining alternative fishery management strategies.

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