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# Movement and behaviour of large southern bluefin tuna (*Thunnus maccoyii*) in the Australian region determined using pop-up satellite archival tags

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## ABSTRACT

Pop-up satellite archival tags (PSATs) were deployed on 52 large (156–200 cm length to caudal fork) southern bluefin tuna (Thunnus maccovii) in the western Tasman Sea during the austral winters of 2001-2005. Southern bluefin tuna (SBT) were resident in the Tasman Sea for up to 6 months with movements away from the tagging area occurring at highly variable rates. The data indicated a general tendency for SBT to move south from the tagging area in the Western Tasman Sea. Four individuals migrated west along the southern continental margin of Australia and into the Indian Ocean. Three individuals moved east into the central Tasman Sea, with one individual reaching New Zealand. We also describe the first observed migration of an SBT from the Tasman Sea to the Indian Ocean spawning grounds south of Indonesia. Individuals spent most of their time relatively close to the Australian coast, with an estimated 84% of time spent in the Australian Fishing Zone. SBT favored temperatures between 19 and 21°C, adjusting their depth to the vertical temperature distribution. Distinct diurnal diving patterns were observed and adjustment of depth to maintain constant ambient light levels over a 24-h period. The findings of this study are a significant advance toward greater understanding of the spatial dynamics of large SBT and understanding the connectivity between distant regions of their distribution.

Key words: habitat preferences, pop-up satellite archival tag, southern bluefin tuna, spatial dynamics, spawning migration

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## INTRODUCTION

Southern bluefin tuna (Thunnus maccoyii) are a large long-lived pelagic predator widely distributed throughout the oceans of the Southern Hemisphere (Caton, 1991; Clear et al., 2000) and the focus of a large, highvalue, multi-national, commercial fishery throughout their range. Genetic evidence indicates a single discrete spawning region, and the distribution of larvae suggest southern bluefin tuna (SBT) are a single population with spawning limited to an area in the northeastern Indian Ocean south of Indonesia (Caton, 1991; Grewe et al., 1997; Farley and Davis, 1998). Adult SBT are assumed to forage throughout the temperate waters of the Southern Hemisphere oceans during the austral winter, migrating to the spawning grounds of the north-western Indian Ocean from spring to autumn (Shingu, 1978; Caton, 1991) before returning to foraging grounds in the following autumn/winter. Individuals do not remain on the spawning grounds over the whole season; instead there is a turnover of fish with the numbers of mature fish peaking in October and February (Farley and Davis, 1998).

Stock assessments suggest that the current population of SBT is at 5-12% pre-exploitation biomass (CCSBT, 2004). However, many key inputs to management are still unknown. Amongst these is considerable uncertainty about the spatial dynamics and timing of spawning migrations. Spawning ground catch data indicate a higher proportion of younger fish in recent years relative to the 1990s, suggesting possible changes in the age distribution of spawning SBT (Farley and Davis, 2005). Stock assessment models assume a knife-edge recruitment of SBT to the spawning stock at the age of 10+ and implicitly assume that the spawning stock is composed of obligate spawners. Although recent studies suggest that recruitment to the spawning stock is more diffuse, occurring from age 10 or older (Davis and Farley, 2001; Schaefer, 2001), few data are available on the frequency of spawning in mature SBT, the fidelity of fish to foraging regions or mixing rates of SBT between these grounds. Current assumptions about the spatial dynamics of mature SBT are derived from interpretation of longline catch data and conventional mark-recapture data studies, mostly on juveniles. Catch data are thought to be biased by spatial contraction and temporal variability in effort and changes to targeting practices (Toscas *et al.*, 2001) and more recently, subject to potential bias due to under-reported catches (CCSBT, 2006). Additionally, conventional tagging relies on accurate reporting of recapture information and minimal non-reporting of recaptures (Hearn *et al.*, 1999). The development of pop-up satellite archival tags (PSATs), which transmit data from the fish without the need for the tag to be recovered, provide fishery-independent methods for assessing movement in pelagic fish (Gunn and Block, 2001).

Although this technology has been widely utilized on other bluefin species (genus *Thunnus*) (Lutcavage *et al.*, 1999; Block *et al.*, 2005; Wilson *et al.*, 2005), the deployment of PSATs on SBT has been limited. Four tags deployed on large SBT in the region of the spawning grounds north of  $20^{\circ}$ S (Itoh *et al.*, 2002) demonstrated movements south from the spawning ground over periods of a few days to 3 months. Three individuals undertook south-westerly movements into the Indian Ocean and the fourth moved into an area south of the Australian continent. Given the small number of releases and the short tag-attachment durations of those PSATs deployed, it is difficult to infer much regarding the movement patterns of large SBT.

Critical gaps currently exist in our knowledge and understanding of the movements, residency, regional fidelity and spawning dynamics of older SBT. These gaps inhibit accurate assessment of stock status and also management within regional fisheries. Here we report on the results of pop-up satellite archival tagging of large SBT in the Tasman Sea and their dispersal from these waters into the Southern Ocean, providing an important first step toward greater understanding of the spatial dynamics of SBT in the Australian region.

#### **METHODS**

### Tagging operations

Pop-up satellite archival tags (PAT2: N = 11, PAT3: N = 8 and PAT4: N = 33; Wildlife Computers, Redmond, WA, USA) were deployed on large SBT in the waters of the western Tasman Sea in the austral winters of 2001-2005. Fish were caught during commercial long line operations, with those in good condition led into a tagging cradle and then lifted on board the vessel. Females sampled from the spawning ground demonstrate 50% maturity at a length of 154 cm<sup>1</sup> (Farley and Davis, 1998); we therefore chose only fish greater than 154 cm length to caudal fork (LCF) for tagging.

In 2001 and 2002 tags were rigged with a single titanium anchor connected via a 400-lb monofilament tether to the corrodible release pin of the PSAT. In 2003-2005 nylon umbrella-style anchors (Domeier et al., 2005) were used as primary anchors. An additional double-barbed nylon dart tip crimped to a 50-lb monofilament loop was attached as a secondary anchor to further secure the PSAT and to minimize any lateral tag movement. The primary monofilament leader on all tags was fitted with a depth-release device (RD-1500, RD-1800; Wildlife Computers) designed to prevent implosion of the tag at great depth. The primary anchor was inserted into the dorsal musculature at the base of the second dorsal fin following several other studies (Lutcavage et al., 1999; Stokesbury et al., 2004). The secondary anchor was inserted into the dorsal musculature in line with the dorsal finlets. Each tag was printed with reward and return information. The deployment position was recorded using the vessel's onboard GPS system.

#### Data and analyses

We programmed PSATs to record pressure (depth), temperature and light at 60-s (N = 50) or 120-s (N = 2) intervals. To provide a mix of higher resolution, short-term data specific to management applications (see Hobday and Hartmann, 2006) and lower resolution longer-term data capable of capturing broader movements, tags were programmed to release from the fish after 30 days (N = 3), 60 days (N = 4), 90 days (N = 1), 180 days (N = 7), 300 days (N = 1)and 365 days (N = 35). After release, tags floated to the ocean surface and transmitted a summary of their archived data via the Argos satellite service (Service Argos, Toulouse, France). Due to limited transmission bandwidth, data collected by the PSATs were summarized into 1-h (N = 1), 4-h (N = 22), 8-h (N = 20)and 12-h (N = 7) time periods prior to transmission. The summary data for each time period consisted of distributions of the proportion of time-at-depth (TAD) and time-at-temperature (TAT) and temperature-depth profiles. For those PSATs recovered, the full archived dataset was downloaded from the tag. To avoid possible behavioural changes imposed by the process of tagging, only those data collected from tags

<sup>&</sup>lt;sup>1</sup>Schaefer (2001) quotes the figure 164 cm FL. We conservatively chose the lower of these.

at liberty for more than 14 days were included in analyses.

#### Age classification of SBT

To determine whether tagged SBT would be classified as recruited into the spawning stock (as per recent management assumptions), we derived age estimates for each individual using the cohort slicing method. This method is used in Commission for the Conservation of Southern Bluefin Tuna (CCSBT) stock assessments (Preece *et al.*, 2004) and assigns an individual to an age cohort using length-at-age growth curves (Laslett *et al.*, 2002).

#### PSAT attachment duration

The rate of premature tag shedding was examined by normalizing all tag deployments to a nominal start day and plotting the proportion of tags remaining attached to SBT as a function of days attached. We fitted intercept-free regressions of the form:

 $\ln(\text{proportion tags shed}) = \mu \times \text{days attached}$ 

to examine the shedding rate.

#### Location estimates

Daily positions derived from each tag were calculated using a heuristic algorithm (cf., Teo et al., 2004; Shaffer, 2005) that combined light and temperature data. Longitude was estimated using proprietary software (WC-GPE.1.02.0000; Wildlife Computers). Daily estimates of sea surface temperature (SST) were derived from SSTs reported by the tag where the depth of the SST observation was less than 5 m. These were checked for outliers (i.e., extreme temperatures  $> 35^{\circ}$ C) and erroneous measurements were replaced by linear interpolation using the 3 points either side of the gap. A loess smoother (Venables and Ripley, 1997) was applied to the SST to reduce variability in the SST series. Remotely-sensed SST values using MCSST/AVHRR data (PO.DAAC, 2001) for 0.5° of longitude either side of each longitude estimate were then compared to SST values reported by the PSAT. Sea surface temperature values between 50°S and 10°S for each longitude estimate were gridded into cells of 0.25° latitude and the number of matches to the observed PSAT SST was counted in each latitudinal cell. Matches were defined as instances when the tag SST was within 0.1°C of the remote sensing SST. To reduce the number of unrealistic positions generated by spatially-distant matches to SST values, we constrained the distance an individual could move each day by weighting the latitudinal cell frequencies by a function assumed to represent the likelihood of a

movement between consecutive positions. A lognormal distribution

$$\Pr(\text{distance};\mu,\sigma) = (x\sigma\sqrt{2\pi})^{-1}\exp(-\ln(x-\mu)^2/2\sigma^2)$$

was used to model the probability of distance moved. This weighting allows longer distance movements but with lower weight than shorter distance movements. The parameters  $\mu$  and  $\rho^2$  were set at the values  $\mu = 4$ and  $\rho^2 = 1$ . Using the formula for the expectation from the lognormal distribution, E(distance) = $\exp(\mu + \frac{1}{2}\rho^2)$ , the highest weightings are given to movements of approximately  $150 \text{ km day}^{-1}$ , or approximately 0.97 body lengths s<sup>-1</sup> in accordance with published swimming speed estimates for a 170-cm tuna (Bushnell and Jones, 1994; Lutcavage et al., 2000). The latitude cell with the combination of the highest number of matches and weights was considered to be the most probable position. This process was initialized at the known tag-release position. We evaluated the results of our method by comparing the geolocation estimates with transmitted pop-up locations where the last estimated position was no more than 2 days prior to the first transmission date of each PSAT. To derive the minimum distances traveled, we calculated the distance of a simplified and idealized track from the tagging release area to the pop-up point utilizing the 'tracker' tool in the GIS software MAN-IFOLD 6.50 (Manifold Net Ltd., Carson City, NV, USA). This approximates the minimum 'biological distance' that must be traveled by the SBT from the tagging locations to the spawning grounds.

#### Habitat preferences and behaviour

Aggregate time-integrated indices of temperature and depth preferences were constructed by calculating the median TAD and TAT value in each histogram bin. Empirical cumulative distribution functions were calculated from the median proportion in each bin and used to estimate the expected proportion of time in a given depth or temperature range. These were matched to location estimates to examine spatial patterns in depth and temperature preferences.

#### RESULTS

A total of 52 pop-up satellite archival tags were deployed on SBT 156–200 cm LCF (mean  $\pm$  SD: 173.7  $\pm$  9.5 cm – all estimates hereafter are mean  $\pm$  SD unless otherwise stated) estimated to be aged 9–20 yr (15.3  $\pm$  3.1 yr; Table 1). The cohort slicing method utilized in CCSBT stock assessments assigned 50 of the 52 individuals tagged to the spawning stock. Of the 52 PSATs deployed, data were retrieved from 44

	Releases		Pop-up transmissions						
Tag	Date	Latitude (°S)	Longitude (°E)	LCF (cm)	Programmed Duration	Age (yr)	Date	Latitude (°S)	Longitude (°E)
2001									<u> </u>
28703	13 Jul 2001	33.42	151.55	170	300	14	16 Jul 2001	33.38	151.85
28701	13 Jul 2001	35.88	151.57	175	30	16	19Jul 2001	35.90	153.02
28707	13 Jul 2001	35.22	151 53	190	60	20	07 Aug 2001	37 32	154 12
28708	13 Jul 2001	35.22	151.53	158	60	10	27 Jul 2001	37.43	156.62
13274	15 Jul 2001	35.58	151.60	178	180	10	20 Jul 2001	35.17	152.43
13275	13 Jul 2001	35.60	151.60	200	180	20	13 Aug 2001	33 77	153.12
2002	15 Jul 2001	55.00	191.00	200	100	20	15 Aug 2001	55.12	155.12
2002	27 1.1 2002	35.02	151.65	157	30	10	20 1 1002	35.07	152.68
20709	27 Jul 2002	35.02	151.05	157	50	10	20 Aug 2002	35.07	152.00
13272	27 Jul 2002	35.08	151.65	105	60	12	06 Sep 2002	36.82	152.10
20926 2003	27 Jul 2002	35.12	151.67	173	90	15	Failed to transr	nit	
13279	10 Jul 2003	35.98	150.96	171	30	14	06 Aug 2003	34.71	152.27
13273	10 Jul 2003	35.98	150.94	187	60	20	07 Sep 2003	33.72	153.32
20890	10 Jul 2003	35.97	150.85	200	180	20	03 Aug 2003	30.81	153.80
30466	10 Jul 2003	35.97	150.85	186	180	20	14 Oct 2003	35.55	154.75
20914	20 Jul 2003	36.82	150.77	175	180	16	Failed to transr	nit	
20924	28 Jul 2003	35.05	151.80	160	364	10	Failed to transr	nit	
30465	28 Jul 2003	35.05	151.80	168	364	13	24 Jap 2004	42 50	123.18
18564	28 Jul 2003	35.10	150.82	178	180	10	$\frac{1}{1}$ Jan 2004	38 16	122.10
20891	07 Aug 2003	34.23	151.77	165	364	19	16 Sep 2003	30.60	154.96
20071	01 Hug 2005	51.25	191.77	105	501	12	10 000 2005	50.00	15 1.90
2007	27 Jun 2004	34.18	151.87	176	180	17	21 Oct 2004	40.73	140.12
13035	27 Juli 2007	34.13	152.80	170	364	16	13 Dec 2004	42.80	153 37
42026	05 Jul 2004	24.15	152.00	172	264	10	15 Dec 2004	42.00	155.57
43930	05 Jul 2004	34.10	152.00	102	264	15	15 Jul 2004	30.41	155.79
43937	05 Jul 2004	34.18	152.90	182	364	20	04 Sept 2004	33.45	157.86
43925	12 Jul 2004	34.67	153.15	175	364	16	26 Jul 2004	32.55	154.61
43926	12 Jul 2004	34.67	153.15	169	364	13	03 Feb 2005	17.72	111.07
43927	12 Jul 2004	34.67	153.15	183	364	20	14 Jul 2004	33.97	155.24
43928	13 Jul 2004	34.65	153.27	170	364	14	14 Jan 2005	34.87	111.90
43929	13 Jul 2004	34.65	153.27	174	364	16	08 Nov 2004	43.25	150.31
43931	13 Jul 2004	34.65	153.27	169	364	13	19 Nov 2004	42.55	163.88
43932	13 Jul 2004	34.63	153.27	169	364	13	15 Jul 2004	33.59	155.05
43933	14 Jul 2004	34.68	153.23	176	364	17	Failed to transmit – 172 day		days data
43034	15 Jul 2004	34.62	153 15	173	364	15	20 Jul 2004	34 51	152 11
43045	10  Jul  2004	34.07	151.08	175	364	17	$\frac{29}{13}$ Dec 2004	J4.51 44.60	172.11
42046	30 Jul 2004	34.97	151.90	171	364	20	Eailed to transm	44.00	140.00
42042	30 Jul 2004	25.00	151.96	169	264	12	15 NL 2004	1111	159.60
43943	51 Jul 2004	35.00	151.95	109	304	15	15 Nov 2004	44.01	156.09
43941	08 Aug 2004	34.70	152.72	172	364	15	29 Dec 2004	41.46	144.12
43942	08 Aug 2004	34.82	152.95	173	364	15	15 Jan 2005	44.24	146.26
43939	29 Aug 2004	36.42	152.90	175	364	16	27 Nov 2004	40.80	133.59
43940 2005	28 Aug 2004	36.37	152.87	170	364	14	30 Dec 2004	42.95	149.35
53269	07 Jul 2005	34.48	151.55	170	364	14	27 Jul 2005	34.51	153.39
53270	21 Jul 2005	32.24	153.82	177	364	18	Still at liberty	-	
43944	21 Jul 2005	32.89	153.68	173	364	15	10 Dec 2005	43.58	147.78
46336	22 Jul 2005	32.40	153 59	163	364	11	29 Oct 2005	40 54	137.08
46337	22 Jul 2005	32.10	153 55	171	364	14	13 Sep 2005	33 37	155 11
46330	22 Jul 2005	32.55	153 53	172	364	15	21 Sep 2005	37.21	154 02
46340	$01 \Delta_{112} 2005$	35.13	152.15	187	364	20	02  Sep  2005	34.67	153 / 3
10040	01 Aug 2003	JJ.1J	192.19	107	JUT	20	02 Sep 2003	JUI	177.47

Table 1. Release and pop-up details for PSATs deployed on SBT in the western Tasman Sea 2001-2005.

Table	1.	Continued.

	Releases	Pop-up transmissions							
Tag	Date	Latitude (°S)	Longitude (°E)	LCF (cm)	Programmed Duration	Age (yr)	Date	Latitude (°S)	Longitude (°E)
46342	19 Aug 2005	35.68	153.60	168	364	13	20 Oct 2005	43.91	147.64
46343	19 Aug 2005	35.68	153.60	185	364	20	21 Nov 2005	41.17	150.53
46350	19 Aug 2005	35.68	153.58	178	364	19	27 Dec 2005	41.60	140.92
46351	21 Sep 2005	36.22	152.52	157	364	9	23 Sep 2005	34.82	153.11
46353	21 Sep 2005	36.13	152.40	156	364	9	Failed to transmit		
53263	21 Sep 2005	36.11	152.34	164	364	11	06 Feb 2006	38.33	140.67
53264	22 Sep 2005	35.97	153.05	172	364	14	Failed to transmit		

(84.6%; Table 1) via Service Argos with data retrieved from one recovered PSAT which failed to transmit. A total of two PSATs were recovered after washing up on land.

#### PSAT attachment duration

All PSATs detached prematurely, transmitting 1– 362 days prior to the programmed deployment day. Tag attachment durations varied considerably both within and between deployment years, ranging from 2 to 206 days, with considerably better tag retention in years where secondary anchors were used (Fig. 1). The proportion of the intended deployment period achieved ranged from 0.01 to 0.98 (Table 2). Trends in the overall rate of tag loss (Fig. 1) were described by a negative exponential relationship, ln(proportion tags attached) =  $\mu \times (\text{days attached})$  (adjusted  $R^2$ : 0.97,  $F_{1,39} = 1,535$ , P < 0.001). This model estimated the slope coefficient to be -0.02 (SE:  $\pm 0.001$ ) and an attachment 'half-life' (the number of days at which 50% of the tags are likely to remain attached) of 35.4 days (Fig. 1).

#### Geolocation accuracy

Adequate light and SST data were available for the calculation of position estimates for 40 SBT. Of these, 36 were at liberty for periods greater than 14 days and position estimates calculated constituted 5.2-92.6% of the total time tags were at liberty ( $50.7 \pm 21.3\%$ ). Comparison of position estimates calculated via geolocation with a final pop-up position derived from Argos was restricted to 25 PSATs, due to a lack of SST



**Figure 1.** (a) Normalized tag loss rates by deployment year. (b) The overall normalized rate of tag loss through time. The dashed lines indicate the 'half-life' of the PSAT (time till 50% of tags detatched). Tag data from 2002 was not included due to small sample sizes.

	Deployment perio	d (days)	Attachment per	riod (days)	Proportion of period attached		
Year (N)	Mean ± SD	Range	Mean ± SD	Range	Mean ± SD	Range	
2001 (6)	135.0 ± 103.5	30-300	16.2 ± 46.1	2–31	$0.22 \pm 0.13$	0.01–0.42	
2002 (3)	$60.0 \pm 30.0$	30-90	$32.5 \pm 66.1$	24-41	$0.74 \pm 0.08$	0.68-0.80	
2003 (9)	211.3 ± 127.3	30-364	$83.3 \pm 63.3$	24–180	$0.57 \pm 0.36$	0.10-0.98	
2004 (20)	354.8 ± 54.1	180-364	99.1 ± 12.0	3-206	$0.30 \pm 0.20$	0.01-0.64	
2005 (14)	$364.0 \pm 0.0$	364	69.7 ± 11.5	2–142	$0.21 \pm 0.13$	0.01-0.39	
Total		30–364	70.8 ± 61.0	2–206	$0.33 \pm 0.25$	0.01–0.98	

Table 2. Deployment periods and attachment durations achieved by PSATs deployed on SBT in the western Tasman Sea 2001–05.

data for latitude calculation, compromised light data resulting in highly erroneous longitude calculation, or data transmission failure. The median distance or position error ( $\pm$  SD) between the two final positions was calculated to be 161.9  $\pm$  230.6 km (range 23.1–866.3 km, N = 25).

#### Migration and residency patterns

Individuals were resident in the western Tasman Sea from June through to December, predominately in an area bounded by 30-40°S and 150-160°E (Figs 2 and 3). The period spent within this region ranged from 34 to 55 days, with individuals moving out of the region as early as September and as late as December, although most individuals had moved out of the region by October. Five individuals undertook movements east into the central Tasman Sea, with one moving to south-western New Zealand coastal waters before returning to the western Tasman and finally moving east of Tasmania. Two SBT returned to the western Tasman Sea before moving south to an area east of Tasmania (Figs 2 and 3), with one transiting to the north-west of Tasmania. PSATs on the remaining two detached before movement out of the Tasman Sea could be discerned.

Considerable time was spent west and north-west of Tasmania (Figs 2 and 3). Movements into this region from the deployment area occurred as early as September and as late as January. The time taken to reach the area north-west of Tasmania from the deployment area averaged  $26.8 \pm 19.5$  days (range 3–66 days).

Individuals were widely dispersed throughout the southern margins of Australia during the summer months. Fish that moved into the western Australian area were aged 13–19 yr (14.8  $\pm$  2.9 yr) and ranged in size from 168 to 178 cm LCF (173.7  $\pm$  9.6 cm). These individuals reached western Australian waters at varying times throughout November and December, taking 36–84 days to reach the area after departing the

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western Tasman Sea. Of those SBT tracked into the waters south-west of Australia, one travelled into what is regarded as the region of the spawning grounds at 17.72°S, 111.07°E (Fig. 3), whereas two SBT made easterly movements (possibly indicating initiation of eastward return movements) after periods of residency south-west of Australia (Figs 2 and 3). By estimating the total distance from the western Tasman Sea to the area of the spawning grounds using an idealized track around the Australian continent and Tasmania, the SBT which migrated to the spawning ground traveled a distance of  $\sim$  9000 km in 113 days, resulting in an average movement rate of  $\sim 80$  km day<sup>-1</sup>. Movement of the SBT migrating along the western coast of Australia from an area south of Cape Leeuwin at approximately 36°S to the final pop-up position on the southern spawning grounds totaled 1550 km traveled over 26 days. This is equivalent to an average distance traveled of 59.6 km day $^{-1}$ .

Although limited by small sample sizes, no relationship between the size of individual SBT and the extent of their westward movements was apparent. It is also interesting to note that the majority of position estimates (84%) were in the Australian Fishing Zone (AFZ) and thus relatively close to the coast and shelf. Also, there was little indication of residency in the Great Australian Bight (GAB) – an area of large juvenile SBT aggregations during the summer months (Caton, 1991).

#### Habitat preferences and behaviour

Time spent at depth by tagged SBT largely reflected temperature preferences of  $< 18-20^{\circ}$ C (Fig. 4), with the majority of time spent at < 200 m and the highest proportion of time spent at < 50 m. The PDT data showed that SBT experienced minimum and maximum ambient water temperatures of 2.6–30.4°C (Fig. 4) with a median maximum temperature of 18°C (inter-quartile range: 15.4–19.4°C) and a median



Figure 2. (a) Deployment locations of PSAT-tagged SBT in the western Tasman Sea. (b) Deployment-to-popup displacements (c) position estimates of SBT at liberty between 2001 and 2006 Coloured by month.

minimum temperature of 15°C (inter-quartile range: 12.2–17.4°C). The cumulative distribution function of time-at-temperature from all individuals pooled, estimated that SBT occupy waters of < 18.5°C for 30% of the time, at or below 20°C for 50% of the time and at or below 21°C for 90% of the time observed (Fig. 4c).

Individuals spent time in waters deeper than 200 m and cooler than 20°C primarily in three localized areas: the western Tasman Sea centered on the deployment area, the eastern Tasman Sea and the region between 135 and 145°E north-west of Tasmania (Figs 5 and 6). Time spent in waters > 20°C was mostly near the eastern Australian coast in the Tasman Sea and on the spawning grounds in the Indian Ocean (although these data come from a single individual). The fine scale depth and temperature data from the two recovered PSATs reflect the depth and temperatures experienced from transmitted PSAT data (Fig. 7). Depth data recovered from both tags showed that SBT spent greater than 90% of their time in waters shallower than 250 m. Relative to the other individuals, PSAT 43933 spent considerably more time at depths deeper than 400 m and colder than 10°C during the summer when it was resident off the west coast of Tasmania.

#### Spawning ground habitat data

The SBT that migrated to the spawning ground (PSAT 43926) traversed several different water masses during its migration. Whilst in the western Tasman Sea, temperatures were largely restricted to 15–20°C and waters less than 200 m depth (Fig. 7). On initiating southward movement, the SBT encountered variable surface temperatures ranging from 10 to 20°C. Throughout the waters south of Australia, time



**Figure 3.** Individual tracks of SBT for which PSATs remained attached for > 14 days separated into regions of movement and residency outside of the western Tasman Sea region: (a) central and western Tasman Sea; (b) Southern Ocean and (c) Southern/Indian Oceans.

spent in waters deeper than 250 m increased and, in association, temperatures experienced decreased, with waters of  $10-15^{\circ}$ C experienced more frequently (Fig. 7). The depth and temperature experienced by this individual shifted just prior to reaching tropical water masses in mid-January, with increased time in surface waters (< 150 m) punctuated by dives greater than 500 m. Sampled temperature in the region of the spawning grounds was typified by warm waters up to 28°C.

#### Diurnal depth preferences

Lengthy periods of diurnal diving behaviour were displayed in the recovered archival data (Fig. 8). Whereas depths frequented during the day were quite variable (ranging from 150 to 600 m), both SBT favored waters less than 50 m at night during these periods. Diurnal diving behaviour associated with time spent in waters deeper than 400 m, was observed for periods of up to 2 weeks at a time and resulted in SBT

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spending periods of over 10 h in water temperatures less than 10°C and as low as 7°C. Periods of diurnal diving behaviour resulted in SBT remaining at more or less constant ambient light levels (Fig. 8).

#### DISCUSSION

This study provides the first substantive, fishery-independent, observations of the movement of large SBT. The duration of residency of individual SBT, both within and beyond the western Tasman Sea, was highly variable, as was the extent of movements. The data suggest that migration schedules can be highly plastic in nature and could depend on a complex of factors including the status of energetic reserves. The relationship between energetic reserves and condition has been examined by Golet *et al.* (2007) who found significant declines in lipid content over a decadal period in Atlantic bluefin tuna, resulting in possible asynchronous maturity schedules.

**Figure 4.** The average proportion of time spent at (a) depth and (b) temperature, and (c) the cumulative distribution function of the proportion of time spent at temperature for southern bluefin tuna tagged in the western Tasman Sea 2001–2005. The median proportion of time spent within each histogram bin is given in blue.



Depths and temperatures experienced by SBT were variable, although spatially coherent, suggesting that thermal preferences may be driven by proximate factors such as forage availability rather than thermal tolerances. This agrees with Schick *et al.* (2004) who found that the locations of schools of Atlantic bluefin were not related to the locations of fronts but instead may have been influenced by unobservable prey distributions. Care must be taken in drawing conclusions about those factors driving SBT movement and behaviour. **Figure 5.** The proportion of time spent in temperatures (a)  $< 15^{\circ}$ C, (b) between 15 and 20°C and (c) in temperatures  $> 20^{\circ}$ C in relation to the estimated position of SBT tagged in the western Tasman Sea 2001–2005.



Although there was a general pattern of movement south from the tagging area, around Tasmania and into the Southern Ocean, many tags detached prematurely, resulting in a reduced capability of describing movement and habitat beyond the Tasman Sea region.

#### PSAT attachment duration

The problem of achieving long-term PSAT attachments was the single largest hindrance to accumulating long-term data on the movements and habitat preferences of SBT. To attain a more comprehensive understanding of movement patterns of large SBT, improved attachment durations are critical. Incorporation of a secondary anchor into deployments coincided with a considerable increase in attachment duration, a finding supported by a number of other studies utilizing similar secondary anchors (H. Dewar, National Marine Fisheries Service, La Jolla, CA, USA, personal communication). However, the increased attachment durations coincident with the

**Figure 6.** The proportion of time spent in depth ranges (a) 0–50 m, (b) 50–200 m (c) 200–400 m (d) 400–600 m and (e) 600–1000 m in relation to the estimated position of SBT tagged in the western Tasman Sea 2001–2005.



use of our secondary anchors are correlative and not causative. Other factors, such as the expertise of the tagger or variability in the reliability of the tags, may have also contributed to attachment durations.

Determining whether the performance of attachments achieved in this study are comparable to those achieved elsewhere on bluefin species is difficult due to a lack of published data; commonly the achieved attachment duration is published but the intended deployment time is not (e.g., Stokesbury et al., 2004). However, failure of tags to remain attached until programmed release dates has been widely reported elsewhere (Domeier et al., 2003; Gunn et al., 2003; Horodysky and Graves, 2005; Wilson et al., 2005) and is a common problem in studies utilizing PSATs. Maximum attachment durations achieved in this study were considerably shorter than those reported elsewhere [206 days in this study, compared to 371 days in Stokesbury et al. (2004), 304 days in Wilson et al. (2005) and 261 days in Block et al. (2005)]. A number of factors may contribute to reduced attachments including anchor and tether design, tag attachment methods and/or physiological and behavioural differences between species resulting in differences in tissue rejection of anchors or greater wear on attachment points and tethers.

#### Geolocation accuracy

The errors calculated around the final PSAT position estimates in this study compare well to the estimates of geolocation error calculated elsewhere (e.g., Teo et al., 2004; Sibert et al., 2006a) and indicate that the magnitude of errors are sufficiently small for inference of large-scale movements. Comparison of the end points of the track with Service Argos pop-up positions may well be optimistic. Tags floating at the surface of the ocean are likely to be easier to geolocate compared to a tag attached to a tuna. However, we are confident that conclusions about the timing of migrations and duration of residency in various areas are valid at the large scale we consider, despite being obviously noisy estimates of the true movement path. Further improvement to statistical geolocation methodology (e.g., Royer et al., 2005; Lam et al., 2008) is likely to increase the accuracy of position estimates and allow for more detailed characterization of movement and habitat usage. Importantly, advances on current geolocation methods would allow for statistically rigorous characterization of the uncertainty in the location estimates.

#### Habitat preferences and behaviour

Individuals tagged in this study clearly demonstrated a preference for waters at 18–20°C, similar to that observed in juvenile SBT (Gunn and Block, 2001) and other bluefin species (Block *et al.*, 2001; Marcinek *et al.*, 2001; Stokesbury *et al.*, 2004; Kitagawa *et al.*, 2006). However, large SBT can clearly withstand much lower temperatures for sustained periods, spending periods of over 10 h at temperatures less than 10°C.



Therefore thermal preferences are unlikely to solely reflect the physiological tolerance of SBT, but might reflect the physiological limitations of forage species. Tuna are widely documented to associate with fronts and transition zones (Laurs and Lynn, 1977; Olson, 2001; Polovina et al., 2001; Royer et al., 2004). However, the factors driving this association are still largely unknown (Kirby et al., 2000). Frontal areas are often associated with biomass maxima, concentrating chlorophyll production and associated secondary productivity. Gunn and Young (1999) hypothesized that SBT use warm-core eddies and the warm side of fronts as thermal refuge after periods of foraging in colder waters. Use of such oceanographic features to trade-off forage availability against thermoregulatory requirements has been postulated for other species of tuna (Neill et al., 1976; Sund et al., 1981), whereas others have hypothesized that this association is strictly related to the aggregation of forage species only (Brill and Lutcavage, 2001; Brill et al., 2002; Royer et al., 2004). Whether or not this association has links to thermoregulatory Figure 7. Hourly mean temperature in 5-m depth bins from full archival records retrieved from PSATs deployed on southern bluefin tuna in the western Tasman Sea: (a) tag 30466 and (b) tag 43933. (c) Temperature and depth data and (d) monthly temperature depth profiles of SBT 43926 which migrated from foraging grounds in the western Tasman Sea to the area of the spawning grounds in the Indian Ocean.

requirements, the long forays into cool water demonstrated by SBT in this study represent a physiological capability which may allow this species to capitalize on prey concentrations (when they are present) by maximizing the amount of time spent in these frontal and eddy regions. Diurnal patterns in diving behaviour observed in tuna species, including bigeye tuna (Musyl et al., 2003), Atlantic bluefin tuna (Lutcavage et al., 2000; Schick et al., 2004; Gutenkunst et al., 2007) and Pacific bluefin tuna (Kitagawa et al., 2001) have similarly been associated with the movement of forage species either through direct tracking of prey or tracking of particular light levels which may be easiest for ambushing or detecting prey (Warrant, 2000; Brill et al., 2002). Similar behaviour has been observed in several other species such as broadbill swordfish (Carey and Robison, 1981) and bigeye thresher sharks (Nakano et al., 2003; Weng and Block, 2004) and has been postulated to be related to vertical migration dynamics of the deep-scattering layer. The changes in diving behaviour on a diurnal scale associated with relatively



**Figure 8.** (a) Instances of diurnal diving behaviour resulting in the maintenance of a constant light level in the tag 30466 in August 2004 (top) and tag 43933 in July 2004 (bottom). Depth readings are presented in blue and light readings in grey. (b) Detail of a period of diurnal behaviour in tag 43933 (left panel) with depths during the day in grey and at night in black with the proportion of time at depth during the day (open circles) and night (filled circles) on the right.

constant light levels, as observed in this study, suggest that light may play an important role in determining the foraging depth of SBT.

#### Behaviour on the spawning ground

Although limited, the data obtained from the one individual tracked to the spawning grounds provides an interesting insight into the behaviour of SBT both during migration to the spawning grounds and whilst in the area of the spawning grounds.

The diving behaviour of this individual differed markedly between regions, with the fish demonstrating relatively consistent diving behaviour ranging down to 500 m whilst in the Southern Ocean, much deeper diving behaviour in the Indian Ocean and surfacerelated diving behaviour in the region of the spawning grounds. This cessation of deeper diving and a transition to surface-related behaviour appeared to be associated with the occurrence of surface temperatures greater than 24°C. Such surface-related behaviour is similar to that documented by other SBT in the spawning ground region (Itoh *et al.*, 2002) and is

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consistent with suggestions that spawning occurs in surface waters (Davis and Farley, 2001). Additionally, it appears consistent with the vertical movements observed in spawning Atlantic bluefin (Teo et al., 2007). Reasons for the change from occupying depths shallower than 500 m to much deeper diving when moving from the Southern to the Indian Ocean are unclear but may be associated with changes in prey species targeted and in associated changes in prey species distributions and/or changes in the thermal properties of the water masses experienced. The deeper diving demonstrated by this SBT (and, in association, the increased time spent in cooler waters) might have been avoidance of warm tropical surface water. Teo et al. (2007) found that spawning Atlantic bluefin in the Gulf of Maine displayed deep diving en route to spawning regions preceding a period of shallow diving. This was hypothesized to be either a thermoregulatory response or a means to reduce energetic demands by avoiding stronger currents. However, much more data are required to characterize the vertical distribution of SBT in this region.

#### Migration and residency patterns

Although only one SBT was observed to migrate between the Tasman Sea and the spawning grounds, this directly demonstrates connectivity over large spatial scales within the SBT spawning stock. Daily movement rates and the scale of this migration are consistent with those observed in other *Thunnus* species (Mather *et al.*, 1995; Block *et al.*, 2001, 2005). Furthermore, the movements observed in this study were consistent with genetic analyses concluding a single mixed stock (Grewe *et al.*, 1997).

The trigger for movement of SBT away from their winter foraging grounds in the Tasman Sea may be linked to seasonal changes in oceanography. During the austral spring, warm waters associated with the East Australian Current extend down the eastern Australian coastline producing areas of productivity which may move suitable foraging areas for SBT southward. Seasonal upwelling events also begin in the waters to the north-west of Tasmania, increasing productivity in this region and further west into the eastern margins of the GAB throughout spring, summer and early autumn months (Schahinger, 1987; Herzfeld, 1997; Kämpf et al., 2004). The area off the south-west of Australia is also a region of seasonal productivity, largely driven by mixing of the southern boundary of the Leeuwin Current waters and cooler Southern Ocean waters (Pearce and Pattiaratchi, 1999). This region supports a number of fisheries of small pelagic species which may serve as an important foraging area for large SBT. Sub-adult SBT have been observed to switch preferred prey species between areas of residency (Young et al., 1997) and their movements between areas have been hypothesized to be triggered by a drive to capitalize on concentrations of small pelagic fishes (Young et al., 1996). Movement of large SBT may not only be driven by reproductive requirements but also by differential distribution of prey resources.

It is notable that the position estimates from this study suggest that SBT spend the vast proportion of their time on continental shelf areas – 84% of geolocation estimates were within the AFZ. This appears to be in contrast with juvenile SBT, who regularly make cross-basin movements into the Indian Ocean (Gunn and Block, 2001), and catch records show that SBT are caught as far south as 50–55°S (Shingu, 1978). A number of factors may contribute to this perceived high residency in shelf and AFZ waters. First, light-based methods of geolocation are subject to a number of sources of error (Welch and Eveson, 1999). Although we were able to compare position estimates derived using geolocation methods with end points derived from Argos locations, determination of the accuracy position estimates is somewhat limited. Argos locations are subject to varying degrees of error themselves (Hays et al., 2001) and position estimates determined using light and water temperature collected at the water surface after a tag has surfaced cannot be considered to be typical of light and temperature data collected from the animal. As a result, positions estimates inside the AFZ may actually have been outside. However, when considering movements across large spatial scales, those data collected from the SBT that migrated westward clearly indicate extended residency within the western Tasman Sea region and in shelf areas. Secondly, the attachment durations of the PSATs deployed may bias estimated residency periods somewhat. With extended attachment periods the extent of migrations away from shelf areas would no doubt become clearer.

Considerable variability in dispersal rates and movement paths resulted in SBT tagged in the same area being widely dispersed throughout southern Australian waters during the austral summer. All tagged SBT were within the size range observed in the Indonesian spawning ground catches (Farley and Davis, 1998) and only one individual was considered not to be fully recruited to the spawning stock according to methods used in previous CCSBT stock assessments. Such wide dispersion, the lack of coherency in movements and the duration of residency periods in the Southern Ocean and Tasman Sea, relative to the timing of spawning ground abundance peaks, hints at the possibility that reproductively mature SBT may not spawn annually. This possibility has been raised in other tuna species (Sibert et al., 2006b). However, before definite conclusions can be made on spawning participation in SBT, information from longer-term deployments is needed to clearly establish the spatial dynamics of spawning-sized fish. Furthermore, the two peaks in spawning ground abundance (Farley and Davis, 1998) may indicate variable timing of migrations that may be due to spatial structuring within the stock. It is possible that fish observed to be south of Australia when their tags detached in late summer could have continued on to spawn. The movement patterns observed in our study are also consistent with other studies suggesting an older age/size at maturity (Farley and Davis, 1998; Schaefer, 2001) than the current CCSBT spawning classification.

The data collected in this study represent a major step towards reducing uncertainty about the spatial dynamics of a large over-exploited pelagic predator. At the same time, they raise further questions as to

spawning dynamics and the location of other important foraging areas for this species in the Australian region. Despite the limitations of the technology used to collect these data (limited attachment durations, data transmission/reception capacities and geolocation error), determining such life history aspects would be difficult without the use of PSATs. Fisheries data are unable to provide detailed movement data and in the case of adult SBT there have been very few conventional tagging data collected from which to infer movements. Deployment of tags in other areas throughout the range of SBT and across wider temporal periods (not only the austral winter) would serve to address problems associated with attachment durations and also help to define the connectivity of SBT in different fishery areas such as the Australian and South African regions. Furthermore, continued comprehensive data collected across a multi-year period would serve to establish inter-annual variability in SBT habitat preferences and provide important inputs into management regimes such as the spatial management models used in the western Tasman Sea.

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