



Modelling surfacing behaviour of southern bluefin tuna in the Great Australian Bight

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ABSTRACT

Large numbers of juvenile southern bluefin tuna (SBT; *Thunnus maccoyii*) migrate into the warm shelf waters of the Great Australian Bight (GAB) each austral summer. Whilst in the GAB, they aggregate in schools that spend substantial periods in the surface layer of the water column. In this study we investigate biological, temporal and environmental factors influencing this surfacing phenomena using an extensive archival tagging dataset collected between 1998 and 2011. High frequency data on the vertical movement of SBT collected by these tags were used to calculate the proportion of time fish spent in the shallowest 20 m during each day and night period. Estimates of fish location derived from light sensor data on the tags allowed us to investigate the influence that local environmental conditions had on a fish's surfacing behaviour. Although there is high variability in surfacing behaviour within and between individuals, some general patterns emerge. There are clear diel differences in surfacing, with the proportion of time fish spend at the surface tending to be high during most days and either very high (> 90%) or very low (< 10%) during most nights. Complex relationships were found between surfacing behaviour and the environmental variables considered (sea surface temperature, chlorophyll, salinity and wind speed). The results from this study have relevance to the commercial purse-seine fishery targeting surface schools of SBT in the GAB during the austral summer, as well as the scientific aerial survey conducted each summer that collects data on sightings of surface schools of SBT in order to derive a relative abundance index used directly in management.

1. Introduction

The Great Australian Bight (GAB), a large open bay off the southern coast of Australia (Fig. 1), is an important region for juvenile southern bluefin tuna (SBT; *Thunnus maccoyii*). Large numbers of age 1–5 fish migrate into the warm shelf waters each austral summer, where they feed on abundant small pelagic fish such as sardines (Ward et al., 2006). Juveniles generally arrive in the GAB between November and January and leave between March and May, spending the winter either in the Indian Ocean or Tasman Sea before returning to the GAB for the following summer (Basson et al., 2012). This cycle continues until the fish are 4–5 years old, after which they disperse throughout southern temperate waters of the Pacific, Indian and eastern Atlantic Oceans (Basson et al., 2012; Bestley et al., 2009; Hobday et al., 2015).

A conspicuous feature of the behaviour of SBT whilst in the GAB is their tendency to aggregate in large schools that spend substantial periods in the warm surface layers of the water column. The precise reasons for this surface activity are unclear, but it may be a form of behavioural thermoregulation which increases body temperature, with

associated increases in digestive throughput (Gunn and Block, 2001a). This is consistent with juvenile SBT undergoing marked seasonal growth, with growth rates during the summer months being the highest (Eveson et al., 2004; Polacheck et al., 2004).

A large-scale commercial purse-seine fishery operates in the GAB during the summer months (primarily Dec–Mar), catching surface schools of SBT. Spotter aircraft are employed by the fishery to assist vessels in locating surface schools (Basson and Farley, 2014). In addition, a scientific aerial survey is conducted each year in the GAB from January through March in which spotters search for surface schools of SBT (Eveson and Farley, 2016). The data collected are used to estimate an index of relative abundance of juvenile SBT, which forms a key input to the model used by the international organisation responsible for the management of SBT to set a global catch limit (Hillary et al., 2016). Having a reliable index of juvenile abundance in the model increases the probability of management meeting its rebuilding target, which is critical given the highly depleted level of the stock (Hillary et al., 2016). Both the purse-seine fishery and the aerial survey rely on the availability of SBT in surface waters, and could benefit from a better

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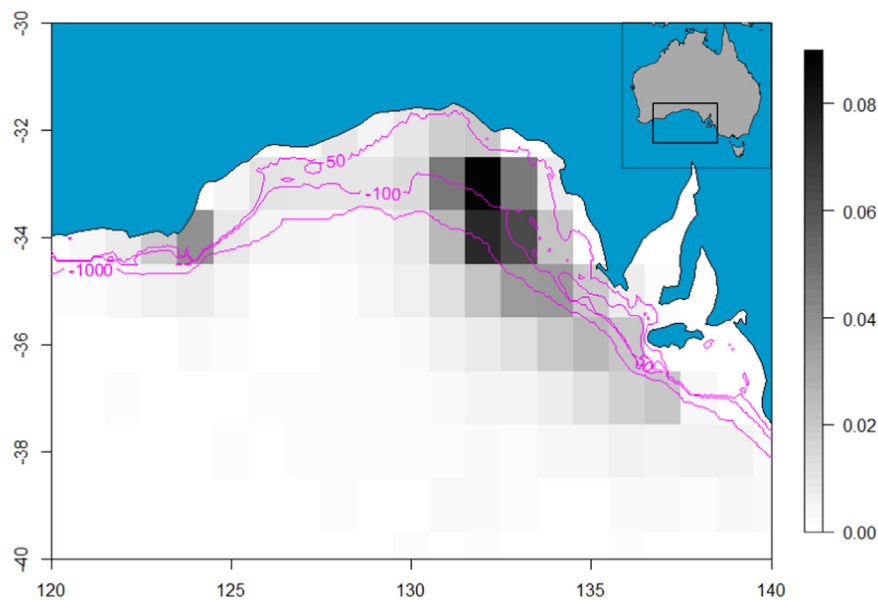


Fig. 1. Density plot of fish position estimates in the Great Australian Bight (defined here as 120–140°E, 30–40°S) during January–March of 1998–2011. Shading indicates the proportion of the most probable position estimates falling in each $1^\circ \times 1^\circ$ grid square. The 50, 100 and 1000 m depth contours are overlaid (pink lines).

understanding of the factors influencing surfacing behaviour. For example, if catch rates or spotting rates are low, this could be due to low abundance of fish in the area, or to fish being deeper than the fishery or the survey can detect; knowing what variables correlate with surfacing behaviour could help tease these competing hypotheses apart.

As part of a broader investigation of the marine ecosystem in the GAB (Baghurst et al., 2017), in this study we investigate the influence that a number of biological, temporal and environmental factors have on the surfacing behaviour of juvenile SBT in the GAB. To do so, we make use of a substantial archival tagging dataset from juvenile SBT that were tagged and recaptured between 1998 and 2011. Archival tags provide high frequency records of the vertical movement of SBT in the water column, allowing us to calculate the average time fish spend at the surface in a given time period and its variability.

Several studies have considered the vertical distribution of tuna in relation to biological factors such as age or size, and temporal factors such as time of day, time of year and moon phase (Bestley et al., 2009; Kitagawa et al., 2007, 2000; Matsumoto et al., 2013a, 2013b; Wilson et al., 2005), but only a few have related it to environmental variables other than water temperature (Arrizabalaga et al., 2008; Lam et al., 2014). One of the reasons for environmental variables not being included in models of vertical distribution is that estimates of geographical location (“geolocation”) from light measurements on archival tags can have large uncertainty (Gunn and Block, 2001a; Hill and Braun, 2001; Musyl et al., 2001), and therefore the environment that the fish was in at any given time has not been known with sufficient accuracy or precision. Geolocation methods have advanced in recent years to use more statistically rigorous methods (e.g. state-space models, likelihood methods) that allow for reliable quantification of the uncertainty in location estimates (Basson et al., 2016; Nielsen et al., 2006; Nielsen and Sibert, 2007). Furthermore, these methods can incorporate external information such as ocean temperature and bathymetry to be compared against tag-measured temperature and depth data in order to provide location estimates with greater accuracy and precision. Thus, we had sufficient confidence in the fish location estimates used in the current study to relate surfacing behaviour of juvenile SBT to environmental variables not measured on the tag, such as chlorophyll, salinity and wind speed, and, importantly, to take into consideration uncertainty in the location estimates when doing so (as detailed in Section 2.3).

2. Methods

2.1. Archival tagging data

A total of 805 archival tags (Wildlife Computers, Redmond, Washington, USA, model Mk7 or Mk9) were deployed on juvenile SBT (47–120 cm) between 1998 and 2011. Fish were tagged throughout their geographical range at different times of the year, namely, in waters south of Australia in Dec–Apr ($n = 555$), east of South Africa in Nov–Dec ($n = 27$), in the southeast Indian Ocean in Jun–Aug ($n = 154$) and in the Tasman Sea in Apr–Jul ($n = 69$). The tags record light intensity, depth, external water temperature and internal peritoneal cavity temperature at intervals ranging from every 20 s to every 4 min depending on the tag model and generation. As of July 2016, 156 tags had been returned, of which 100 were used in our analysis (data could not be downloaded from 29 tags due to battery or sensor failure, and an additional 27 of the Mk7 tags had to be omitted due to a fault in their thermistor causing erroneous external temperature readings).

2.2. Geolocation

Position estimates were obtained twice daily (at dawn and dusk) using the “twilight likelihood” (TL) method of Basson et al. (2016), which uses the light data from each twilight event to estimate the likelihood (i.e., the probability density) of the light data given any location on the globe. Similar to other geolocation methods, this method requires light readings at the surface, so for diving animals such as SBT, the observed light data needs to be corrected for light attenuation due to water depth. We used a depth correction method (CSIRO unpublished data) similar to that developed by Ekstrom (2002). This method requires that data associated with day (i.e., the period between dawn and dusk) be identified; therefore, an initial step involves using a hidden Markov model (HMM) to estimate the probability of each light observation corresponding to day. These probabilities were used not only in the geolocation method, but also in our analysis of surfacing behaviour to classify tag readings of depth and temperature as belonging to: dawn (probability of day between 0 and 1 and increasing), day (probability of day equal to 1), dusk (probability of day between 0 and 1 and decreasing), or night (probability of day equal to 0).

The likelihood surfaces from the TL method were input to a grid-based HMM to estimate the most probable track of each fish (see Basson

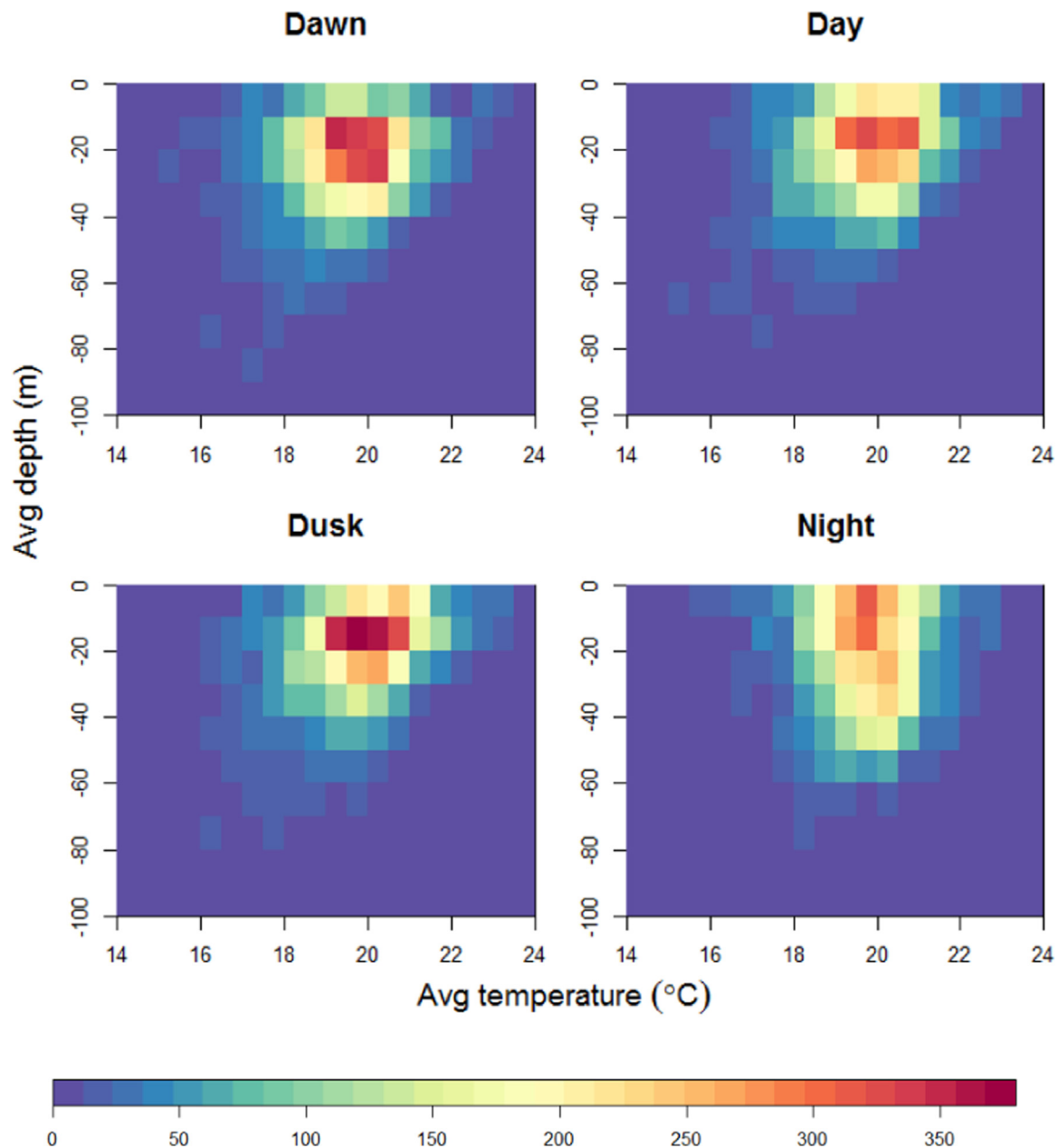


Fig. 2. Two-dimensional frequency plots of average depth (m) and average external temperature ($^{\circ}\text{C}$) during each period (dawn, day, dusk, night) for fish in the GAB during Jan-Mar. The colour bar indicates the number of observations in each bin.

et al., 2016). In this HMM, the location of a fish at each twilight (constrained to a discretised $1^{\circ} \times 1^{\circ}$ latitude-longitude grid) was the hidden/latent state, and the probability of moving between states (i.e. grid cells) was assumed to be a random walk. Any observational data which may be informative in determining position estimates can be included in the gridded HMM in the form of a likelihood. Here, average temperature recorded on the tag when the fish was in the top 20 m during each twilight event was calculated as an estimate of sea surface temperature (SST) and compared against remotely-sensed SST data, and maximum depth recorded on the tag during each twilight event was compared against bathymetry data.

The output of the HMM is the posterior probability of the fish being in each possible grid cell on the globe (excluding any cells that correspond to land masses) during each twilight event. Because of the large number of tags, many with long deployments, we used a $1^{\circ} \times 1^{\circ}$ grid for computational tractability. For each tag, a “most probable track” was estimated by taking a weighted average of all the grid latitudes and

longitudes using the posterior probabilities at each twilight as the weights. Note that the most probable position estimates were used only for plotting purposes; we used the posterior probability surfaces for extracting environmental covariates to relate to fish surfacing probabilities (see below for details).

2.3. Modelling surfacing behaviour

Because the focus of this study is on the surfacing behaviour of SBT in the GAB during the austral summer, we only considered data where the most probable position estimate fell within the region $120\text{--}140^{\circ}\text{E}$, $30\text{--}40^{\circ}\text{S}$ in the months of January through March (Fig. 1). These months were chosen because they encompass the peak period when juveniles are resident in the GAB (see Figure 10.8 of Basson et al., 2012).

The proportion of time that a fish spent at the surface, which we will denote by P_{surf} , was calculated for each dawn, day, dusk and night time

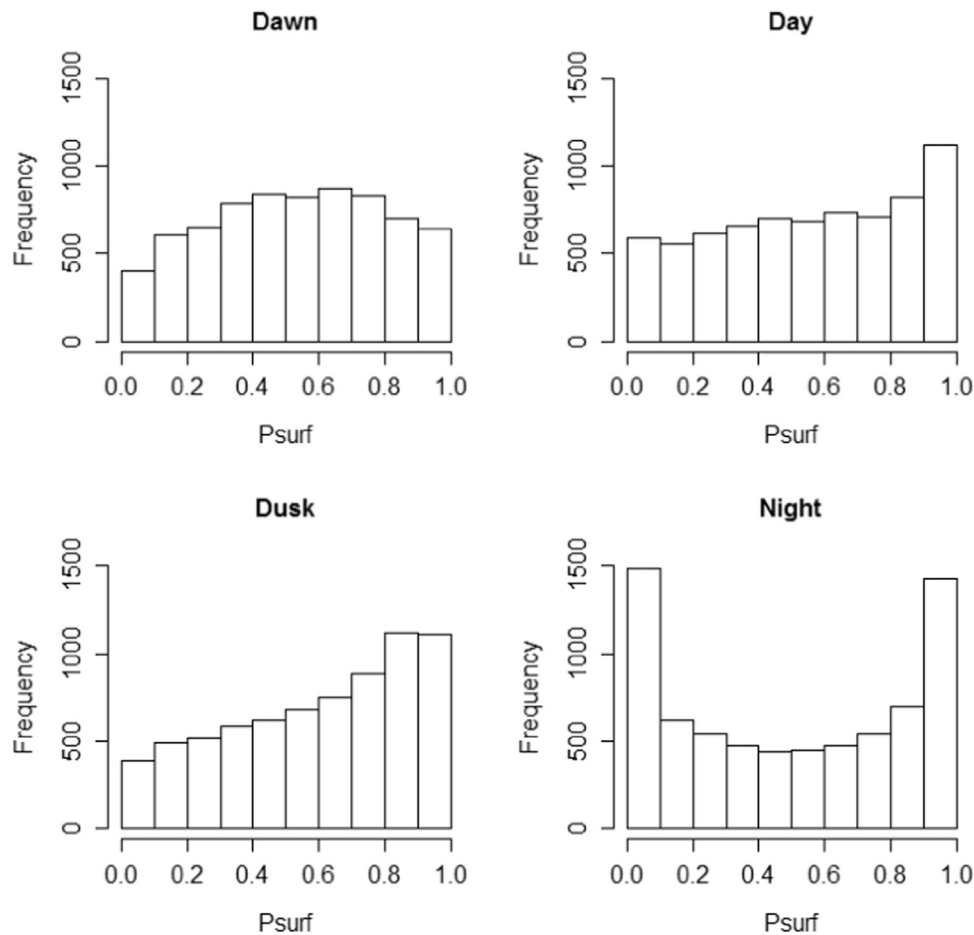


Fig. 3. Histograms of the proportion time spent at the surface (P_{surf}) during each period (dawn, day, dusk, night) for fish in the GAB in Jan-Mar.

Table 1

Summary information for remotely-sensed or derived data products used in our analysis.

Variable	Source	Spatial coverage	Spatial resolution	Temporal coverage	Temporal resolution	Available data [*]	Reference
Chlorophyll a (mg/m ³)	SeaWiFS	Global	0.083° lat x 0.083° lon	Oct 1997-Dec 2010	8 days	38%	NASA Goddard Space Flight Center (2014)
Salinity (psu)	CSIRO Bluelink SPINUP 6.8	Global	0.15° lat x 0.30° lon	Jan 1994 – Dec 2008	1 day	91%	http://wp.csiro.au/bluelink/global/bran/
Wind speed (m/s)	NCEP	Global	2.5° lat x 2.5° lon	Jan 1980 - present	1 day	100%	Kalnay et al. (1996)
Mixed layer depth (m)	CARS	Global	0.5° lat x 0.5° lon	Climatology	1 day [^]	100%	Ridgway et al. (2002)

CARS: CSIRO Atlas of Regional Seas; NCEP: National Center for Environmental Prediction; SeaWiFS: Sea-viewing Wide Field-of-view Sensor.

^{*} Available data refers to the percent of all fish position estimates being included in the model (i.e., in the GAB during Jan-Mar) for which the product had data available.

[^] CARS MLD is available for every day of the year, but since it is a climatology, it is a long-term average of the MLD on a given day of year over all years included in the climatology.

Table 2

Correlation between continuous explanatory variables included in the GAMs using only data from the GAB in Jan-Mar.

	SST	ΔT	MLD	Log(Chl)	Salinity	Wind
SST	1	− 0.514	− 0.056	0.109	0.525	0.022
ΔT		1	0.092	− 0.114	− 0.326	− 0.022
MLD			1	− 0.308	− 0.356	− 0.009
Log(Chl)				1	0.240	0.094
Salinity					1	− 0.015
Wind						1

period as the proportion of tag observations where depth was in the top 20 m. A threshold of 20 m was chosen to define the surface layer because any shallower depth choice omitted a large percent of

observations during the day period, which we believe to be indicative of surfacing behaviour for the purposes of this study (Fig. 2). For instance, experienced spotters operating in the aerial survey and commercial fishery can see fish up to 20 m deep under most conditions (J. Farley, CSIRO, pers. comm.). The relationship between P_{surf} and a number of different explanatory variables was explored using generalized additive models (GAMs). Separate models were fit for dawn, day, dusk and night, but for brevity, only results from the day and night models are presented here. The day period is of greatest relevance for the SBT fishery and the aerial survey; however, surfacing behaviour at night was quite distinct, with a dichotomous high or low proportion of most nights spent at the surface, and provides the most interesting contrast (Fig. 3).

Two types of GAMs were fitted: one type that included only space

Table 3

Significance of covariates included in (a) the spatio-temporal GAMs, and (b) the environmental GAMs fitted to the proportion of time spent at the surface during the day and during the night for fish in the GAB in Jan-Mar.

(a) Spatio-temporal GAM results						
	Day df	Chi-sq	p-value	Night df	Chisq	p-value
Parametric terms[*]						
Month (integer)	2	116.8	0.000	2	2.27	0.321
Smooth terms[*]						
Fish ID	98.0	984.0	0.000	98.0	1029.2	0.000
(Lat, Lon)	28.6	328.8	0.000	28.4	859.6	0.000
(b) Environmental GAM results						
	Day df	Chi-sq	p-value	Night df	Chisq	p-value
Parametric terms[*]						
Age (integer)	4	57.2	0.000	4	125.6	0.000
Smooth terms[*]						
Fish ID	91.0	371.1	0.000	91.0	481.5	0.000
SST	1.0	2.4	0.124	3.8	4.5	0.261
ΔT	3.1	11.7	0.009	3.5	228.3	0.000
Moon fraction	5.5	29.6	0.000	4.1	251.2	0.000
MLD	4.3	45.4	0.000	7.3	26.8	0.000
Log(chl a)	5.0	36.1	0.000	1.0	3.9	0.049
Salinity	4.6	11.6	0.036	6.6	32.0	0.000
Wind speed	7.6	42.7	0.000	1.0	24.1	0.000

* Significance assessed based on Wald chi-square tests.

^{*} Significance assessed based on approximate Wald chi-square tests, conditional on smoothing parameter estimates; see documentation for anova.gam in R package mgcv, and Wood (2013).

and time covariates in order to investigate spatial and temporal patterns in surfacing behaviour, which we will refer to as ‘spatio-temporal GAMs’; and a second type that included only environmental and biological (fish) covariates to investigate possible drivers behind any of the spatial and temporal patterns observed, which we will refer to as ‘environmental GAMs’. Covariates included in the spatio-temporal GAMs were latitude, longitude and month. Covariates included in the environmental GAMs were fish age, moon fraction, sea surface temperature (SST, °C), temperature differential (ΔT , °C), chlorophyll *a* (mg/m³), salinity (psu), wind speed (m/s), and mixed layer depth (MLD, m), details of which are given below. We did not include space-time covariates in the environmental GAMs because doing so could mask the significance of the environmental variables. For instance, if an environmental variable tends to have greater values in the eastern area of the GAB, then any relationship with surfacing behaviour could be explained by a longitudinal effect instead.

2.3.1. Covariates in the environmental GAMs

Fish age, in integer years, was the only biological variable included in the environmental GAMs. The integer age of each fish at the time it was tagged was estimated from its length using the growth curve adopted by the SBT management organisation, the Commission for the Conservation of Southern Bluefin Tuna (Anonymous, 2011; Eveson, 2011). The fish's integer age during each time period it was at liberty was then calculated based on its age at tagging and the time since tagging, assuming a birth date of January 1. For example, if a fish tagged in February 2001 and caught in April 2002 was estimated to be age 2 at the time of tagging, it would be estimated to be age 2 for all time periods until 1 January 2002, at which point it would be estimated to be age 3 for all time periods until recapture.

The only environmental covariate included in the GAMs that was independent of fish location was the fraction of the moon illuminated (from 0 to 1). This was calculated for each observation using the date and standard astronomical algorithms (Meeus, 1998). Of the

environmental covariates specific to fish location, SST and ΔT were derived from data recorded by the tags and, thus, not influenced by uncertainty in location estimates. SST was defined as external temperature when the fish was in the top 20 m, and ΔT was defined as the difference between internal (body) and external (water) temperature. ΔT is intended to be an approximate measure of feeding activity, since visceral warming in SBT has been shown to be an indicator of feeding events (Gunn et al., 2001b). For each fish (i.e. tag), we calculated average SST and average ΔT during each dawn, day, dusk and night time period for which it had data.

The remaining environmental covariates (chlorophyll *a*, salinity, wind speed and MLD) were extracted from externally measured or derived data products that were openly available, had the best spatial and temporal coverage and resolution for our analysis (many products were not available for all the years of our study), and had the least missing observations (Table 1). The spatial resolution of the chosen data products ranged from fine-scale (0.083° grid for SST) to broad-scale (2.5° grid for wind speed). The temporal resolution of all chosen products was daily except for chlorophyll, for which the daily satellite images were very patchy (large areas of missing data) and an 8-day composite product was necessary to get usable data coverage. Even with an 8-day product, chlorophyll data was missing for 62% of the ~28,100 fish locations in our dataset. The remaining sample size (~10,700) was large enough that chlorophyll could still be included in the GAMs; however, to test the sensitivity of the results to excluding so many data points, we also ran the environmental GAMs without chlorophyll. Because the most probable position estimates for a fish can be highly uncertain, it can be misleading to simply extract values of the environmental variables corresponding most closely to these estimates. Instead, values for all locations at which the fish had a non-zero posterior probability of being located were extracted and a weighted average of those values was calculated using the posterior probabilities as weights; a similar approach was used by Heerah et al. (2013) and Lam et al. (2014). This involved first interpolating the raw data from each variable to the same 1° x 1° spatial grid as the posterior probability surface, which we did using the interp.surface.grid function from the fields package in R (R Core Team, 2015). Then, the interpolated data from the closest matching date to the fish location in question were used to calculate the weighted average. For example, for a fish location from dawn of 27 Jan 1998, this meant using the environmental data from 27 Jan 1998 for all variables except chlorophyll, for which the closest matching data was 29 Jan 1998.

2.3.2. Fitting the GAMs

Models were fit using the gam function in the mgcv package (Wood, 2011) for R (R Core Team, 2015), using a beta error distribution. This assumes the P_{surf} data are beta distributed on (0,1). Note that the beta distribution is numerically unstable at exactly 0 or 1. As a simple approach to deal with this, we added (subtracted) a small value (0.001) to any 0 (1) values of P_{surf} , this only applied to 3.5% of the data. In the spatio-temporal GAMs, (latitude, longitude) was included as a 2-dimensional smooth term, and month as a factor. In the environmental GAMs, age was included as a factor, whereas all remaining covariates (SST, ΔT , chlorophyll *a*, salinity, wind speed, MLD and moon fraction) were included as smooth terms. Penalized regression splines were used for the smooth terms, and the degree of smoothness was estimated automatically (these are the default settings of the gam function). Chlorophyll *a* was log-transformed in order to reduce the high degree of right skewness in its distribution. Correlations between pairs of continuous environmental variables were low enough that inclusion of all variables in the GAMs was considered appropriate (Table 2). In both the spatio-temporal and environmental GAMs, an additional variable, fish ID, was included as a random effect to account for the fact that there were multiple observations per fish, and that within-individual residuals are likely to be correlated (see Wood, 2011 for details of how random effects are implemented with the function gam).

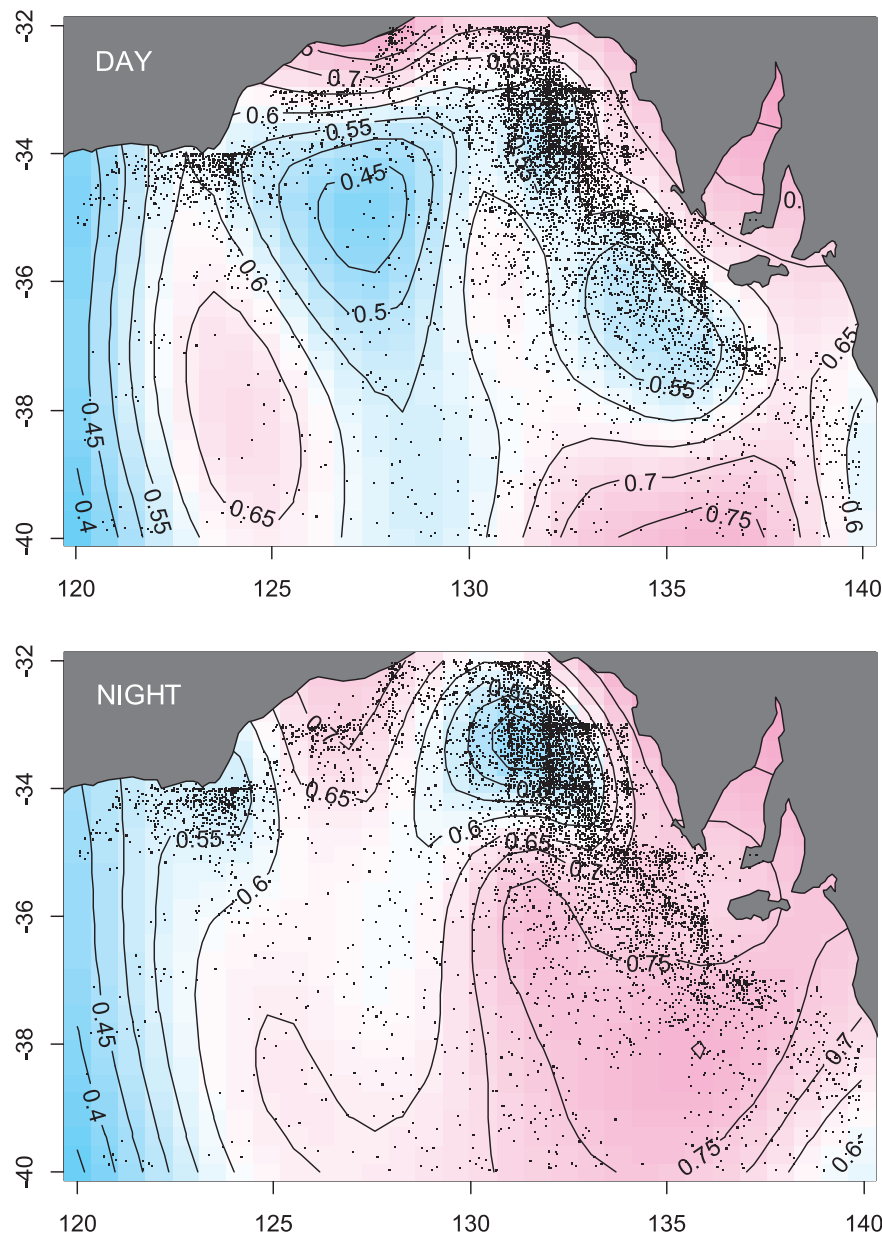


Fig. 4. Spatial maps showing predicted proportion of time spent at the surface (P_{surf}) from the GAMs with latitude x longitude as a 2-dimensional smooth term and month as a factor (set to January for predictions), using data from the day period (top) and the night period (bottom). Blue indicates P_{surf} values < 0.5, pink indicates values > 0.7, and intermediate values are whitish. Black dots show fish locations (most probable position estimates) in the dataset; in areas where the dots are sparse, the GAM results must be interpreted carefully (e.g. the blue area centred around 35°S, 127°E in the day figure for which time at the surface is predicted to be low has very few observations and is an artefact of the GAM spatial prediction).

In the spatio-temporal GAMs, the latitude and longitude values input as covariates are the most probable fish position estimates, which are known to contain varying degrees of uncertainty. Similarly, in the environmental GAMs, the procedure described above to calculate a weighted average of the environmental covariates based on position uncertainty should produce a more robust value for input to the models, but does not account for the fact that the environmental averages corresponding to highly uncertain position estimates will themselves contain greater uncertainty. As such, in both types of GAMs, we down-weighted the contribution to the log likelihood of data corresponding to highly uncertain position estimates (using the weights argument in the gam function). Specifically, we set prior weights equal to the inverse of the square-root of the area of the 70% posterior credibility surface (normalized by the mean of all weights so the overall magnitude of the log likelihood would not change). Thus, position estimates with 70% posterior credibility surface areas of 1, 4 and 9 grid squares were given

relative weightings of 1, 1/2 and 1/3, respectively. While this weighting procedure was somewhat arbitrary, we trialled several variations and the results were similar.

Statistical significance of covariates was assessed using Wald-like chi-squared tests provided by the `anova.gam` function in R (see documentation in R package `mgcv` and references therein). Covariates were considered statistically significant if the p-value was less than 0.01.

3. Results

Of the 100 fish with archival tag data available for our analysis, 99 of them spent time in the GAB during the months of January to March (Fig. 1), ranging from 2 to 272 days over one or more summers (mean = 72.7 days, SD = 51.0 days). While in the GAB, fish were generally found at an average depth of less than 50 m (90% of all dawn, day, night and dusk time periods), and within an average temperature

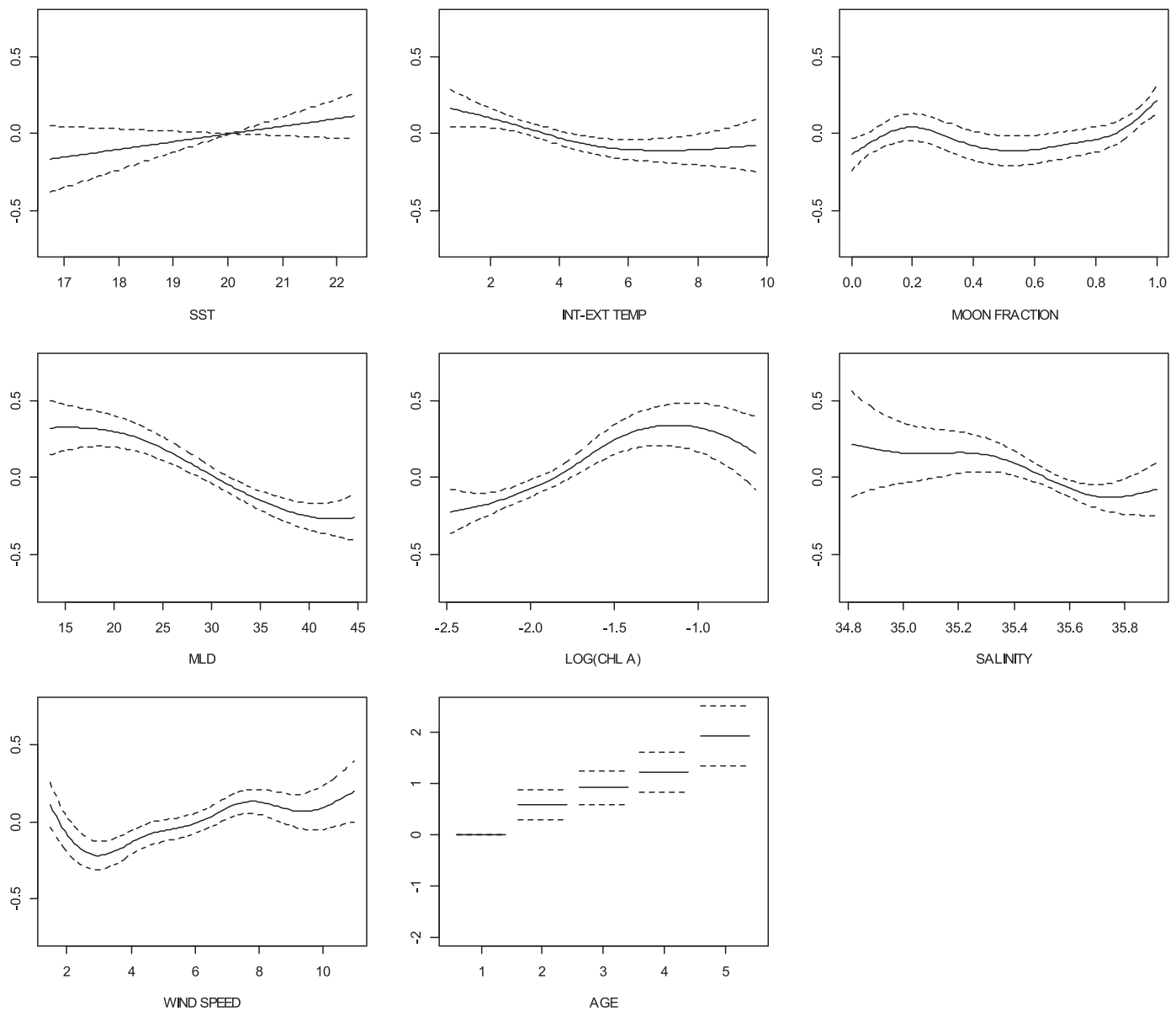


Fig. 5. Plots of estimated partial effects for all terms included in the GAM for the proportion of time spent at the surface (P_{surf}) during the day for fish in the GAB during Jan-Mar. All terms were included as smooths, except for age, which was included as a parametric factor. The dashed lines indicate ± 2 standard errors. (Note that the y-axis limits are different for age than the smooth terms.).

band of 16–23 °C (96% of all time periods) (Fig. 2). Such a shallow average depth could in part be due to the bathymetry of the GAB since coastal waters are less than 50 m deep; however, 98% of the most probable fish location estimates were in waters deeper than 50 m, and 83% were deeper than 100 m (Fig. 1).

The proportion of time that fish spent in the top 20 m (P_{surf}) varied depending on the time of day. For example, during the daytime, the distribution of P_{surf} was fairly uniform with a slight skew towards one (Fig. 3), meaning fish spent anywhere from 0% to 100% of each day period at the surface, with the average being 55.3%. The distribution of P_{surf} for dusk was similar, but with the skew towards one being greater and the average proportion of each dusk spent at the surface being 59.6%. During the night-time, the distribution of P_{surf} was U-shaped, meaning that fish tended to spend very little (0–10%) of a night at the surface or else almost all (90–100%) of a night at the surface (Fig. 3).

In the spatial-temporal GAMs, the month effect was only significant in the day model (Table 3), with a tendency for P_{surf} to decline over summer (average fitted P_{surf} values for Jan, Feb and Mar were 62%, 57% and 48% respectively). In both the day and night models, the

latitude-longitude term was significant (Table 3), but with quite different spatial patterns (Fig. 4). During the day, P_{surf} tended to be similar in all areas where there were a lot of observations (between 0.55 and 0.70), except for inshore, where it tended to be higher. During the night, there is an area roughly delineated by 32–35°S, 129–133°E where fish tended to spend less time at the surface (P_{surf} between 0.4 and 0.65) compared to other areas, particularly to the southeast.

Turning now to the environmental GAMs, all covariates in the day model were estimated to be statistically significant ($p < 0.01$) except SST and salinity (Table 3). The model was fit to over 2500 observations (from 100 fish), so despite being statistically significant, the magnitude of the effects can be small in practical terms (Fig. 5). The variable with the largest effect on P_{surf} was age, with P_{surf} tending to increase as age increased. The environmental variables with the largest effect were log (chlorophyll) and MLD, with P_{surf} increasing as chlorophyll increased and decreasing as MLD increased (Fig. 5).

All covariates in the GAM for the night period were statistically significant ($p < 0.01$) except for SST and log(chlorophyll) (Table 3). Again, the large number of observations being included in the model

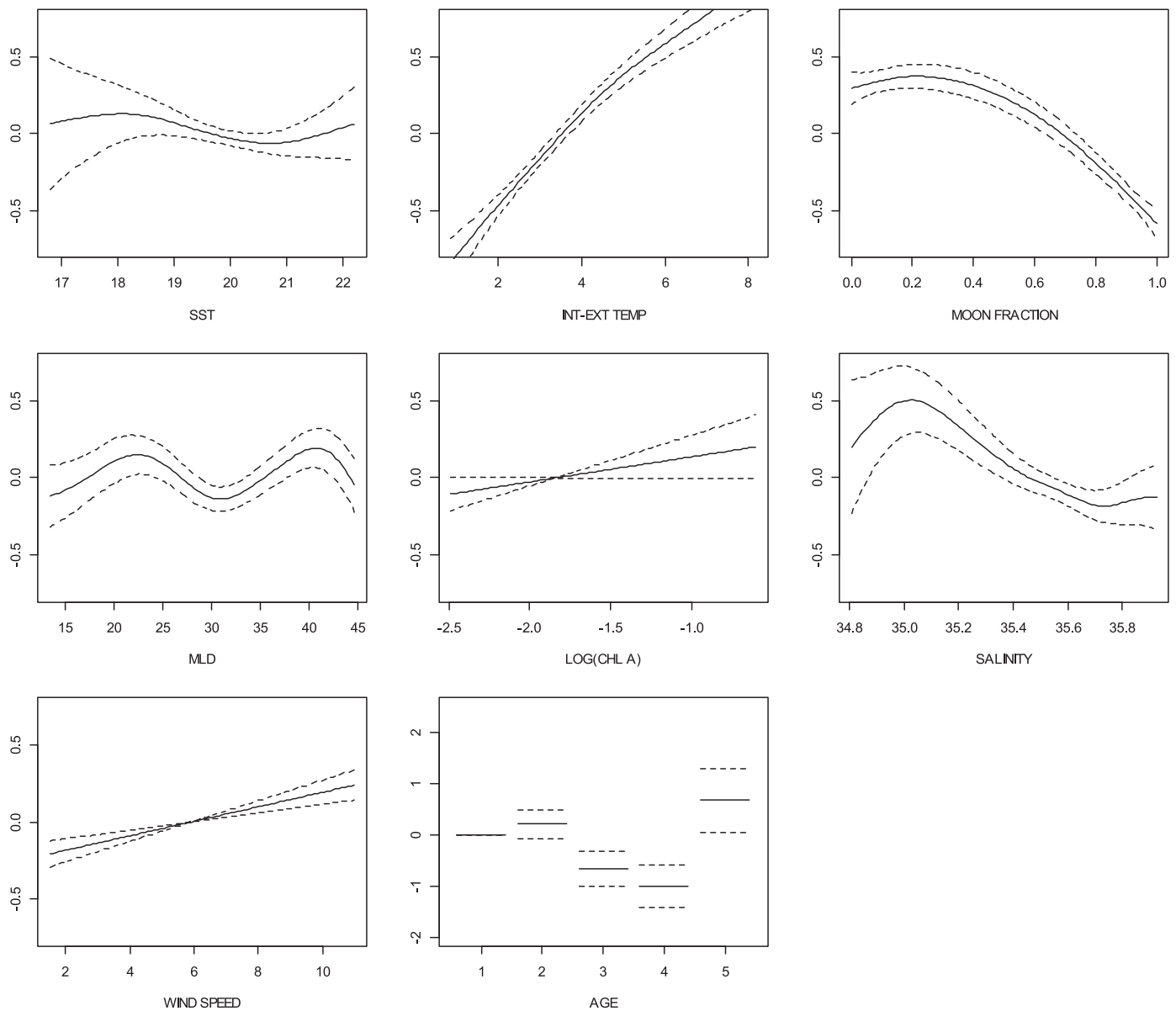


Fig. 6. Plots of estimated partial effects for all terms included in the GAM for the proportion of time spent at the surface (P_{surf}) during the night for fish in the GAB during Jan-Mar. All terms were included as smooths, except for age, which was included as a parametric factor. The dashed lines indicate ± 2 standard errors. (Note that the y-axis limits are different for age than the smooth terms.).

means that not all variables that were statistically significant had a large effect on P_{surf} ; however, for some variables the effect size was large (Fig. 6). Most noticeably, P_{surf} increased markedly as ΔT increased, and decreased as moon fraction and salinity increased. The relationship with age was more complex, but P_{surf} declined between the ages of 2 and 4, which represents over 90% of the data (Fig. 6). The GAM for the night period explained a greater percent of the deviance than the GAM for the day period (49.3% vs. 28.5%), which is congruous with the effect sizes being larger for more covariates in the night model.

Fish ID was highly significant in both the day and night GAMs, indicating there is a large degree of individual variability in surfacing behaviour not accounted for by the other covariates in the models. For example, using the day model to predict the average proportion of a day that each individual fish would spend at the surface when the environmental covariates are fixed at their average values, the predictions ranged from 0.25 to 0.87 (mean = 0.54, SD = 0.09).

In the models without chlorophyll, the amount of data that could be included in the GAMs increased to over 6000 observations, and as a

result, even more covariates became statistically significant. However, in qualitative terms, for both day and night, the estimated effects for all covariates were very similar to the models with chlorophyll (Supplementary Fig. S1).

4. Discussion

Surfacing behaviour of juvenile SBT in the GAB differs during the day and night, with a high proportion of most days spent at the surface, versus a dichotomous high or low proportion of most nights spent at the surface. The results of this investigation suggest that a number of variables influence surfacing behaviour—which ones, and the strength and direction of the relationships, can vary depending on whether it is day or night.

Diel patterns in vertical distribution have been observed in previous studies of SBT (Bestley et al., 2009) and other bluefin tunas (Kitagawa et al., 2007; Wilson et al., 2005), as well as in many other tuna species (Evans et al., 2008; Schaefer and Fuller, 2007; Schaefer et al., 2011)

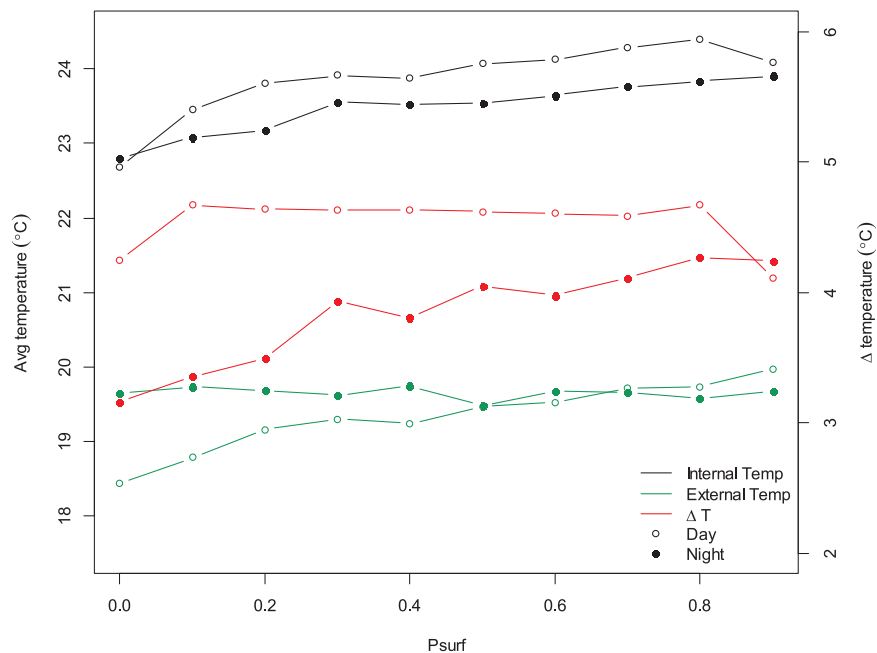


Fig. 7. Average internal temperature (°C, black) and external temperature (°C, green) versus proportion time spent at the surface (P_{surf}) during the day period (open circles) and the night period (filled circles). The average temperature differential, ΔT (°C, red), is plotted on the right y-axis.

and billfish (Evans et al., 2014; Sippel et al., 2011). The ubiquity of diel vertical migration amongst tuna and billfish has been associated with the diel vertical migration of their prey belonging to the deep scattering layer (DSL) (Hays, 2003). Even though much of the SBT data considered here was located in relatively shallow shelf waters (< 100 m), where one might imagine the diel migration of prey to be constrained by bathymetry, the variables we found to influence surfacing behaviour of SBT in the GAB correspond well with this hypothesis. For instance, as the fraction of the moon illuminated increased, the proportion of time SBT spent near the surface at night decreased. This is consistent with SBT tracking their prey since the depth of the DSL is deeper when the moon is brighter (Prihartato et al., 2016), and/or being able to see their prey at greater depths when moon illumination is greater.

Most studies that report diel vertical migrations in tuna (see references above) also report that fish are found in shallower water during the night than day, and that they make deep dives during the day. While this is not the case for SBT in the GAB, it is true for juvenile SBT in the open ocean where, in contrast to their behaviour in the GAB, juveniles spend only a small fraction of the day period in the upper 20 m (see Supplementary Fig. S2).

A strong, positive relationship was observed between the proportion time spent at the surface during the night and the difference between internal (body) and external (water) temperature. On further investigation, we found this was driven by external temperature remaining almost constant, at an average value of ~ 19.6 °C, regardless of the proportion of the night spent at the surface (Fig. 7). This suggests that, during nights that fish spent less time at the surface, they were in locations where temperature remained very warm below 20 m. These locations correspond to the areas identified in the spatial-temporal GAM for the night period as having below average surfacing probabilities (i.e., blue areas in the bottom panel of Fig. 4).

Age was a significant factor in the surfacing behaviour of SBT during both day and night. At night, fish tended to spend less time at the surface between the ages of 2–4. This may be due to older (larger) fish feeding on larger prey items than younger (smaller) fish, noting that, within the DSL, larger organisms are often distributed more deeply than smaller organisms (e.g. Frank and Widder, 2002 and references therein). In contrast, the time spent at the surface during the day increased with age, the reason for which is unknown and would be

interesting to pursue particularly given the opposite would be expected if SBT develop an increased capacity to maintain internal temperatures and buffer cooler conditions with age, as has been reported for Pacific bluefin tuna (*Thunnus thynnus orientalis*) (Kitagawa et al., 2001). Such findings suggest that a broad number of potential environmental and physiological factors (e.g. competition, predation, prey resources, metabolic needs) need to be considered when exploring drivers for behaviour.

There was a significant negative relationship between the proportion of time spent at the surface and MLD in the day period. This is consistent with fish seeking warm surface waters during the day, and being able to find such waters below the surface layer (defined as 20 m) when the MLD is deeper. Furthermore, MLD deepens between January and March in the GAB (mean of 25.0 m, 28.7 m and 38.0 m for Jan, Feb and Mar, respectively, using MLD values at locations in our data set), which explains why the proportion of time fish spent at the surface declined with month in the spatial-temporal GAM for the day period (and why we did not include month as a covariate in the environmental GAMs, because doing causes MLD to be insignificant in the day model).

In terms of oceanographic covariates, time spent at surface had the strongest (positive) relationship with chlorophyll during the day, and with salinity (negative) during the night. The reasons for these relationships are unknown, and likely involve complex interactions between the covariates themselves as well as other variables not considered, such as prey density. Prey density is almost certainly a significant driver in both the horizontal and vertical distribution of SBT in the GAB, but unfortunately prey data across the spatial and temporal range of this study are not available for inclusion in the models.

Data from the aerial survey that operates annually in the GAB to provide an estimate of juvenile abundance of SBT are analysed using a generalized linear model to standardize the number of sightings for environmental variables that might affect the surfacing behaviour of SBT and/or the ability of spotter to see schools of fish (Eveson and Farley, 2016). Two of the most influential factors in the model are SST and wind speed, with the number of sightings increasing as SST increases and decreasing as wind speed increases. The GAM results from this study for the day period are interesting because they suggest SST is not a significant factor in how much time juveniles spend at the surface. Eveson et al. (2015) studied habitat preferences of juvenile SBT in the

GAB and found that fish prefer to be in locations with SST values in the range of 19–22 °C, but the current study suggests that once fish are in locations with those temperatures, the amount of time they spend at the surface does not vary greatly. As for wind speed, the proportion of time spent at the surface during the day does not appear to be greatly influenced by wind speed over the conditions in which the aerial survey operates (wind speed of less than 10 knots, or 5.1 m/s), which may indicate that the decrease in sightings in windier conditions is due more to schools not being visible than to fish not being present at the surface.

The GAB is expected to undergo changes in currents and temperature as the result of global warming (Hobday and Lough, 2011). Furthermore, a number of industries operate in the GAB (e.g., commercial fishing, tourism, shipping, oil and gas operations), and activities associated with these industries may intensify in future. The individual and cumulative effects that these changes could have on the migration of juvenile SBT to and from the GAB, and their surfacing behaviour whilst in the area, are largely unknown. The results of this study provide an important baseline against which future behaviour of SBT can be compared. Of course, such comparisons can only be made if data on the movement and behaviour of SBT in the future exists, highlighting the importance of having a long-term monitoring system.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at <http://dx.doi.org/10.1016/j.dsr2.2018.03.007>.

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