

Annual migrations, diving behavior, and thermal biology of Atlantic bluefin tuna, *Thunnus thynnus*, on their Gulf of Mexico breeding grounds

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Abstract Electronic tags were used to examine the biology of Atlantic bluefin tuna (*Thunnus thynnus* L.) on their breeding grounds in the Gulf of Mexico (GOM). The hypothesis that movement patterns, diving behavior, and thermal biology change during different stages of the breeding migration was tested. Mature Atlantic bluefin tuna tagged in the western Atlantic and the GOM, were on their breeding grounds from February to June for an average of 39 ± 11 days. The bluefin tuna experienced significantly warmer mean sea surface temperatures (SSTs) within the

GOM ($26.4 \pm 1.6^\circ\text{C}$) than outside the GOM ($20.2 \pm 1.9^\circ\text{C}$). As the bluefin tuna entered and exited the GOM, the fish dove to daily maximum depths of 568 ± 50 and 580 ± 144 m, respectively, and exhibited directed movement paths to and from the localized breeding areas. During the putative breeding phase, the bluefin tuna had significantly shallower daily maximum depths (203 ± 76 m), and exhibited shallow oscillatory dives during the night. The movement paths of the bluefin tuna during the breeding phase were significantly more residential and sinuous. The heat transfer coefficients (K) were calculated for a bluefin tuna in the GOM using the recorded ambient and body temperatures. The K for this fish increased rapidly at the high ambient temperatures encountered in the GOM, and was significantly higher at night in the breeding phase when the fish was exhibiting shallow oscillatory dives. This suggests that the fish were behaviorally and physiologically thermoregulating in the Gulf of Mexico. This study demonstrates that the movement patterns, diving behavior, and thermal biology of Atlantic bluefin tuna change significantly at different stages of the breeding migration and can be used to define spawning location and timing.

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Introduction

Atlantic bluefin tuna (*Thunnus thynnus*) have attracted the attention of scientists with their migratory ability, large body size, and endothermic physiology (Mather et al. 1995; Block and Stevens 2001; Graham and Dickson 2004). This species can grow to a length >300 cm, and attain a mass of 680 kg (Magnuson et al. 1994). Atlantic bluefin tuna make rapid, ocean basin-

scale migrations, ranging from cool subpolar foraging grounds to discrete breeding grounds in warm, subtropical waters during the spawning season (Mather et al. 1995; Block et al. 2005). The endothermic physiology of the Atlantic bluefin tuna is thought to allow the species to expand their thermal niche and penetrate into the cold ambient temperatures on their foraging grounds (Carey and Lawson 1973; Neill and Stevens 1974; Block and Finnerty 1994; Block et al. 2001; Graham and Dickson 2004). The use of electronic tags has greatly improved our understanding of bluefin tuna biology on their foraging grounds (e.g., Carey and Lawson 1973; Neill and Stevens 1974; Block et al. 2001, 2005; Gunn and Block 2001; Kitagawa et al. 2004; Stokesbury et al. 2004; Wilson et al. 2005). However, our understanding of their biology during their reproductive period remains relatively poor (Schaefer 2001). In this study, we use electronic tags to examine the biology of the Atlantic bluefin tuna on their breeding grounds in the Gulf of Mexico (GOM).

Atlantic bluefin tuna are known to spawn in two main regions and periods—the GOM from April to June and the Mediterranean Sea from June to August (Magnuson et al. 1994; Mather et al. 1995; Schaefer 2001). In addition, some of the western Atlantic bluefin tuna are likely to spawn in the Florida Straits and Bahamas area (Baglin 1982; Clay 1991; Block et al. 2001). Electronic tagging studies have shown that bluefin tuna tagged in the western Atlantic migrate to the two major spawning grounds in the GOM and the Mediterranean Sea during their respective breeding seasons (Block et al. 2001, 2005; Stokesbury et al. 2004). The bluefin tuna that spawn in the GOM are associated with feeding aggregations in North Carolina, mid-Atlantic Bight, and New England waters during winter and spring (Stokesbury et al. 2004; Block et al. 2005). These fish tend to migrate to their spawning grounds in the GOM from February to June, and exit the GOM by the end of June (Block et al. 2005). During summer and autumn, the bluefin tuna expand their range and can be found in feeding aggregations in the North Atlantic Ocean, ranging from New England waters in the western Atlantic to the Flemish Cap area in the central Atlantic, and the eastern Atlantic (Block et al. 2005).

The International Commission for the Conservation of Atlantic Tunas (ICCAT, <http://www.iccat.es>) currently manages the Atlantic bluefin tuna as two distinct stocks. ICCAT assumes the western Atlantic spawners form a distinct stock from the eastern Atlantic spawners, which spawn in the Mediterranean Sea, and that there is limited mixing between the two stocks across the 45°W meridian (Fromentin and

Powers 2005). However, electronic tagging studies have recently shown that the two stocks are distinct during the breeding periods but mix across the 45°W meridian on their foraging grounds (Block et al. 2005). The western stock of Atlantic bluefin tuna has suffered a >80% decline in spawning stock biomass since 1970 and a 20-year rebuilding plan was enacted in the early 1980s (Magnuson et al. 1994). However, recent assessments indicate that the western stock has continued to decline (ICCAT 2005, p. 81–88). One likely factor contributing to the decline of the western stock is the incidental catch of breeding fish by pelagic longline fisheries operating in the GOM (Block et al. 2005). There is currently no directed fishery for this species in the GOM but observer and logbook data from the National Marine Fisheries Service and scientific longlining data indicate that there is substantial bycatch of Atlantic bluefin tuna in the GOM during the breeding season (Block et al. 2005).

The warm ambient temperatures on their breeding grounds in the GOM potentially present a distinct physiological challenge to these large, endothermic fish (Sharp and Vlymen 1978; Blank et al. 2004; Block et al. 2005; Kitagawa et al. 2006). Electronic tagging studies have shown that Atlantic bluefin tuna can experience very warm water temperatures (as high as 29.8°C) on their breeding grounds in the GOM (Block et al. 2001, 2005). Due to the bluefin tuna's ability to conserve heat, Sharp and Vlymen (1978) hypothesized that the fish may be vulnerable to overheating in warm waters, especially during bouts of intense activity. In a series of laboratory experiments, Blank et al. (2004) have shown that Pacific bluefin tuna cardiac function is extremely temperature sensitive and studies at the cellular level indicate an acute sensitivity to calcium uptake in Atlantic and Pacific bluefin tunas (Landeira-Fernandez et al. 2004; P.C. Castilho, A.M. Landeira-Fernandez, and B.A. Block, unpublished data). At high temperatures > 30°C, bluefin hearts have a reduced calcium uptake capacity. This suggests that cardiac output is reduced at high temperatures. Body temperatures as high as 30.7°C have been recorded by electronic tags inside the peritoneal cavity of Atlantic bluefin tuna in the GOM (Block et al. 2001). If the giant Atlantic bluefin tuna are unable to change their rate of heat transfer and diving behavior in response to warm ambient temperatures, the fish spawning in the GOM during June may become more vulnerable to overheating and hypoxia.

In this study, we used electronic tags to compare the movement patterns, diving behavior, and thermal biology during different phases of the Atlantic bluefin tuna's breeding migration into the GOM. As the

Atlantic bluefin tuna migrate through the Florida Straits to their spawning grounds, we hypothesized that the fish shifts from a migratory phase with an emphasis on movement towards a breeding location, to a breeding phase with behaviors associated with courtship and spawning. The diving behavior of many species of fish changes dramatically during courtship and spawning (Magnuson and Prescott 1966; Colin 1978; Colin and Clavijo 1978; Konstantinou and Shen 1995) and electronic tags have been successfully used to determine the time of spawning in Pacific halibut, based on the changes in recorded diving behavior (Seitz et al. 2005). Since tunas tend to perform courtship and spawn near the surface at night (Schaefer 2001), we hypothesized that the electronic tags would record changes in the Atlantic bluefin tuna's diving behavior during the breeding phase.

We also used electronic tags to examine the thermal biology of the Atlantic bluefin tuna in the GOM. The ambient water temperatures, sea surface temperatures (SSTs), and body temperatures experienced by the fish during the putative breeding phase were compared to the migratory phases. We estimated the whole body heat transfer rates (K) from the ambient and body temperatures recorded by the tags and compared the K from the putative breeding phase to the migratory phases. The results from this study should help identify the physiological challenges faced by this species on their breeding grounds and elucidate the potential strategies used by the fish to overcome these challenges.

Materials and methods

From 1996 to 2004, 772 Atlantic bluefin tuna (*T. thynnus* L.) were tagged with either implantable archival tags (499) or popup satellite archival tags (PAT, 273) in North Carolina, Massachusetts, and the GOM (Block et al. 2005). The experimental procedures have previously been described in detail (Block et al. 1998a, b, 2001, 2005). Five models of archival tags (NMT v1.1 and v1.2, Northwest Marine Technology, USA; Mk7 v1 and v2, Wildlife Computers, USA; and the LTD 2310, Lotek Wireless, Canada) and four versions of PAT tags (Wildlife Computers, USA; hardware versions 1–4) were deployed.

In North Carolina and Massachusetts, the bluefin tuna were caught on rod and reel, brought aboard the vessel and measured (cm curved fork length, CFL). The fish were then tagged with a PAT tag or an implantable archival tag. The PAT tag was attached externally at the base of their second dorsal fins with a

titanium dart and monofilament leader that penetrated to a depth of 14 cm (Block et al. 1998a). The archival tags were surgically implanted into the peritoneal cavity of the bluefin tuna (Block et al. 1998b). In the GOM, the bluefin tuna were caught on commercial longline gear and their sizes were visually estimated. The fish in the GOM were then tagged over the side of the vessel with a PAT tag mounted on an aluminum pole (Block et al. 2005).

Electronic tags and geolocation

The PAT tags recorded ambient temperature, pressure, and light level data every 60 and 120 s. At a preprogrammed date, the PAT tag detached from the fish, surfaced, and transmitted a summary of the data to the Argos system over 6–12 days. If a PAT tag was recovered, the full archival data set consisting of ambient temperature, pressure and light level data every 120 s was retrieved. A proprietary software package from the tag manufacturer (WC-GPE Suite v1.1.5.0, Wildlife Computers, USA) was used to correct for light attenuation and to estimate longitudes from the transmitted light level data. The longitude was estimated from the time of local noon or midnight, using standard astronomical algorithms (Hill 1994; Ekstrom 2004). The PAT tag also transmitted the mean SST and/or PAT depth-temperature (PDT) profile data for each day. The PDT data at 0 m and/or the mean SST for each day were combined with the corresponding light level-based longitude to estimate latitude (Teo et al. 2004; see below).

The LTD 2310, NMT, and Mk7 archival tags were programmed to archive the light level, pressure, peritoneal and ambient water temperatures, every 120 s (LTD 2310 and Mk7) or 128 s (NMT). The LTD 2310 and NMT tags had onboard software that processed the light level and pressure data, corrected for light attenuation, and logged the estimated longitude. The light level data from the Mk7 archival tag were post-processed using a proprietary software package from the tag manufacturer (WC-GPE Suite v1.1.5.0, Wildlife Computers, USA) to correct for light attenuation and estimate the light level longitude. The daily SSTs were extracted from the ambient water temperatures recorded within 1 m of the surface. We compensated for any drift in the pressure sensor prior to extracting the SSTs using the method described in Teo et al. (2004).

The SST data were combined with the corresponding light level longitude estimates to obtain daily latitude estimates. Teo et al. (2004) provided a detailed explanation and analysis of the latitude estimation algorithm. For a given day, the latitude at which the

tag-recorded SSTs best matched the corresponding remotely sensed SSTs, along the light level longitude estimate, was considered the latitude estimate for the day. Based on swimming speeds estimated from acoustic tracking studies (Boustany et al. 2001) and given that the fish could not move over land, the SST matching process for each day was constrained to the area that the fish could have realistically moved. The daily maximum diving depths recorded by the tags were also used to filter the geolocation estimates so that the maximum diving depth did not exceed the known bathymetry (inclusive of error estimates) at the geolocation estimate for the corresponding day. On Atlantic bluefin tuna, archival tags have root mean square (rms) errors of 0.78° and 0.90° for longitude and latitude estimates, respectively (Teo et al. 2004). For PAT tags, the rms errors in the longitude and latitude estimates were 1.30° and 1.89°, respectively (Teo et al. 2004).

For bluefin 98–512, sunrise and sunset diving behavior was used to estimate the longitudes after the light and ambient temperature sensors failed on 2 July 1999. Bluefin tunas exhibit distinct diving behaviors during sunrise and sunset (Gunn and Block 2001; Marcinek et al. 2001; Wilson et al. 2005). Therefore, we used the times of sunrise and sunset diving behavior as proxies for the times of sunrise and sunset. The times of sunrise and sunset diving behavior were fitted to least squares cubic splines (Spline Toolbox, Matlab 7.0.1, The Mathworks). The daily times of local noon were then calculated from the two splines and used to estimate the longitudes using standard astronomical algorithms. The longitudes estimated from diving behavior correlated well with the longitudes estimated from the light level data ($P < 0.001$, $R^2 = 0.628$). The rms difference between the two sets of longitude estimates was 2.9° (17 January 1999 to 2 July 1999). Since the rms error of light based longitudes from archival tags is 0.78° (Teo et al. 2004), a conservative estimate of the rms error of the longitudes derived from diving behavior would be 3.68°. Since longitudes west of approximately 80°W in the Atlantic would indicate that the fish had entered the GOM, this level of accuracy in the longitude estimate was sufficient to determine if the fish had reentered the GOM after 2 July 1999.

Analysis

The geolocations estimated from light and SST data were combined with the corresponding tagging, popup endpoint and/or reported recapture locations to generate a database containing 13,821 geopositions. Based

on this database, 37 Atlantic bluefin tuna were located within the GOM and 28 of these fish returned enough electronic tag data from within the GOM for further analysis (Table 1). The geolocation, depth, ambient and body temperature data during the periods in the GOM were extracted and analyzed.

The movement paths of the Atlantic bluefin tuna were overlaid on ocean bathymetry to visualize the association of the movements with the continental shelf and slope (Fig. 1). We were able to estimate the daily geolocations for 88.7% (417 of 470 days) of the time that the fish were in the GOM. The missing geolocations were primarily due to transmission errors in the PAT tags. For subsequent movement path analysis, the missing geolocations were filled in with interpolated positions, which were calculated as equidistant points along a great circle path between the estimated geolocations.

The daily temperature–depth profiles for the Atlantic bluefin tuna were constructed from the temperature and depth data of the archival-tagged fish and the PDT data of the PAT-tagged fish (Fig. 2). For the archival-tagged fish, the temperature and depth data for each day were fitted to a locally weighted polynomial regression (loess fit) to construct the temperature–depth profiles (Cleveland 1993). For the PAT-tagged fish, the daily temperature–depth profiles were constructed using a broken stick model to linearly interpolate the mean temperatures from the PDT data. The daily temperature–depth profiles and the mean daily SSTs were plotted over time to provide profiles of the distinct water masses experienced by the fish (Figs. 2, 3). The SSTs experienced by the Atlantic bluefin tuna, inside and outside the GOM, were compared using the Kruskal–Wallis test, a non-parametric equivalent of the one-way analysis of variance.

The diving behavior in the GOM was used to divide the period in the GOM into three phases (Fig. 4). The entry phase was characterized by deep diving as the fish entered the GOM and migrated to the breeding grounds. The second phase was a putative breeding phase characterized by shallow oscillatory diving during the night. The final exit phase was similar to the entry phase, with the bluefin tuna exhibiting deep diving (Fig. 4). For each fish, we determined the daily maximum depths during its period in the GOM and filtered the maximum depths using a 3-days median boxcar filter. The maximum depth was used because it was the most common depth data collected and returned by both archival and PAT tags. The overall mean of the filtered maximum depths was calculated, and the central portion of the period in the GOM that was shallower than the mean was considered the

Table 1 *Thunnus thynnus*. Atlantic bluefin tuna that exhibited migrations to breeding grounds in the Gulf of Mexico (GOM) and returned electronic tag data from the GOM

Fish ID	Tag type ^a	CFL (cm) ^b	Tagging date	Tagging location	Popup or recapture date ^c	Popup or recapture location
98–512	A	207	17 Jan 1999	34.53N 76.63W	22 Aug 2000	41.18N 69.10W
99–040	P	230	20 Mar 1999	26.34N 91.26W	20 May 1999	27.91N 91.27W
99–706	P	250	6 Apr 2000	26.53N 91.34W	–	–
99–710	P	220	6 Apr 2000	26.52N 91.37W	4 Jun 2000	29.03N 77.97W
99–588	RP	220	6 Apr 2000	26.49N 91.29W	3 Aug 2000	33.75N 61.90W
99–521	P	240	7 Apr 2000	26.41N 91.42W	–	–
99–725	RP	220	7 Apr 2000	26.45N 91.39W	–	–
99–719	P	210	9 Apr 2000	26.43N 91.26W	7 Jun 2000	25.61N 91.97W
99–680	RP	260	10 Apr 2000	26.43N 91.25W	–	–
99–692	RP	220	10 Apr 2000	26.33N 91.33W	–	–
99–608	RP	240	11 Apr 2000	26.40N 91.27W	–	–
99–609	P	220	4 May 2000	27.63N 87.82W	20 Nov 2000	32.38N 76.25W
99–712	P	230	13 Apr 2001	26.73N 94.49W	–	–
00–715	P	220	17 Apr 2001	26.64N 94.61W	1 Jun 2001	25.44N 91.01W
00–716	P	230	17 Apr 2001	26.67N 94.60W	–	–
99–729	P	220	25 Apr 2001	27.24N 94.02W	–	–
00–1027	P	226	27 Sep 2001	41.12N 69.02W	20 May 2002	40.26N 67.96W
00–1015	P	267	31 Oct 2001	41.30N 68.92W	3 Feb 2002	25.09N 84.22W
02–257	RP	260	11 Apr 2002	27.23N 91.80W	23 Apr 2002	28.03N 85.38W
02–259	RP	220	14 Apr 2002	27.32N 91.18W	21 May 2002	26.93N 85.88W
02–267	RP	250	15 Apr 2002	27.33N 91.21W	26 Apr 2002	28.24N 90.63W
02–270	P	250	20 Apr 2002	27.17N 94.79W	2 Jun 2002	27.79N 76.24W
00–273	P	250	20 Apr 2002	27.17N 94.79W	29 Apr 2002	27.51N 94.77W
02–271	P	240	21 Apr 2002	27.05N 94.85W	19 Jun 2002	27.61N 77.29W
00–295	RP	290	22 Apr 2002	26.98N 94.87W	30 Apr 2002	26.53N 95.66W
A0532	A	208	25 Jan 2003	34.55N 76.32W	12 Oct 2005	44.61N 63.07W
03–251	P	268	16 Jan 2004	34.42N 76.26W	27 Aug 2004	43.23N 67.57W
03–230	P	223	16 Jan 2004	34.42N 76.25W	12 Aug 2004	43.23N 64.83W

^a Two types of tags were used: archival (A) and popup (P) tags. Recovered popup (RP) tags provided data similar to archival tags but without body temperature data

^b Curved fork length (CFL) of bluefin tuna tagged in North Carolina and New England waters were measured to the nearest cm. CFL of bluefin tuna tagged in Gulf of Mexico were visually estimated to the nearest 10 cm

^c Popup dates and locations of tags that had detached from fish >5 days before popoff date, are not reported

breeding phase. Subsequently, the diving behavior from the three phases was visually examined to ensure that the algorithm performed adequately. The unfiltered maximum daily depths for the three GOM phases of each fish were compared using the Kruskal–Wallis test, combined with post hoc Tukey–Kramer multi-comparison tests.

Two measures were used to determine if there was significant site residency or directed movement during these three putative phases in the GOM. The mean squared distance (MSD) from the center of activity is a measure of the dispersion of the locations, with a low MSD indicating high site residency (Schoener 1981; Spencer et al. 1990). The center of activity was calculated as the mean of the geolocations and the MSD of the geolocations from the center of activity was then calculated. The linearity index (LI) is a measure of the linearity of the movement path (Spencer et al. 1990). The LI was calculated as the linear distance between

the endpoints divided by the path distance. A LI approaching one would indicate directed, linear movement while a low LI would indicate a sinuous path. For each fish, the MSD and LI scores within a 5-days boxcar window were calculated and the mean MSD and LI score for each phase and fish were then calculated. The mean MSD and LI scores for the three phases were compared using the Kruskal–Wallis test, combined with post hoc Tukey–Kramer tests.

The SST, depth, ambient and body temperature data from the entry and exit phases were compared with the putative breeding phase. The SST data from all tags were separated into the three phases in the GOM and compared using the Kruskal–Wallis test, combined with post hoc Tukey–Kramer tests. We also used the data from archival and recovered PAT tags to detect diel differences in the diving behavior and temperature during the three phases. The transmitted data from PAT tags were not used because the data were not

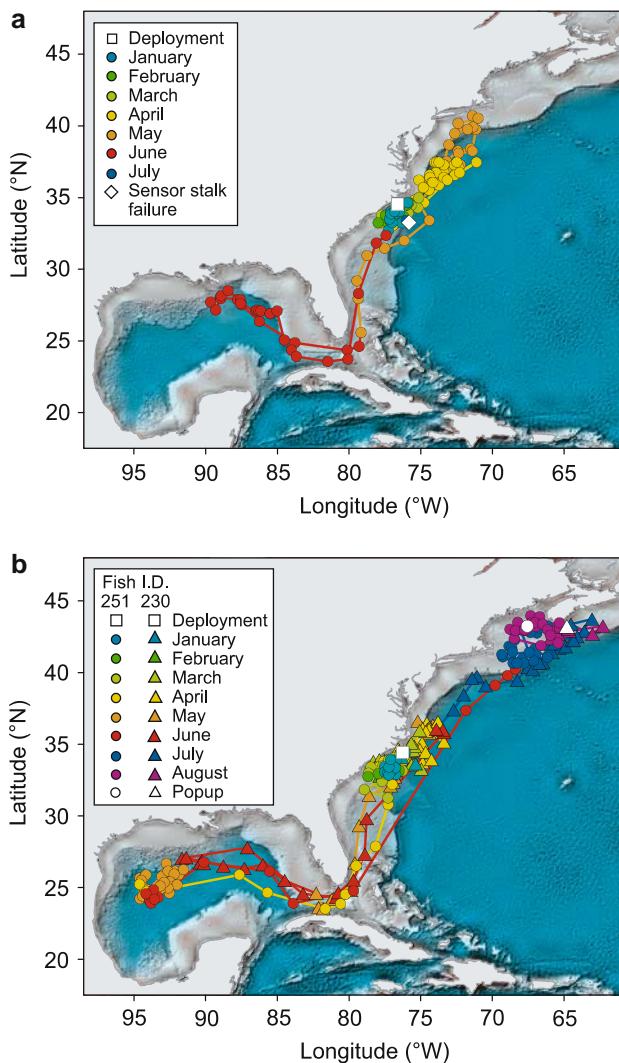


Fig. 1 *Thunnus thynnus*. Tracks of three Atlantic bluefin tuna that were tagged off North Carolina and migrated to the Gulf of Mexico in the spawning season. **a** Track of bluefin 98–512, archival tagged on 17 January 1999. Light level and ambient temperature sensors failed on 2 July 1999. **b** Tracks of bluefins 03–251 (circles) and 03–230 (triangles), both tagged with PAT tags off North Carolina on 16 January 2004

separated into day and night. The depth, ambient and body temperature data from the day and night of the three phases were compared using the Kruskal–Wallis test, combined with post hoc Tukey–Kramer tests. In addition, the mean day and night depths during the breeding phase were related to the mean SST, using robust linear regression.

The whole body heat transfer coefficient (K) of Atlantic bluefin tuna during their period in the GOM was examined in relation to body temperature (Tb) and ambient water temperature (Ta). The tag data from the GOM were first divided into hourly periods. For each period, we assumed that the whole body heat

transfer of the tuna was in non-steady state conditions, where the rate of change of the body temperature, $d\text{Tb}/dt$, can be described by

$$\frac{d\text{Tb}}{dt} = K(\text{Tb} - \text{Ta}) + \frac{d\text{Tb}_{\text{MET}}}{dt},$$

where t is the time interval and $d\text{Tb}_{\text{MET}}/dt$ is the rate of change in the body temperature due to metabolic heat production (Neill and Stevens 1974; Holland et al. 1992; Dewar et al. 1994). We used an optimization approach to estimate K and $d\text{Tb}_{\text{MET}}/dt$ for each period (Neill and Stevens 1974; Holland et al. 1992). The Tb for each period was modeled using the above equation and we used non-linear least-squares optimization (Levenberg–Marquardt method, Dennis 1977) to estimate the K and $d\text{Tb}_{\text{MET}}/dt$ that would provide the smallest sum of squares between the observed and modeled Tb (Optimization Toolbox, Matlab 7.0.1, The Mathworks). The estimated K values were examined in relation to the corresponding mean Tb and Ta. In addition, the K values from the breeding phase were compared with the entry and exit phases using the Kruskal–Wallis test, combined with post hoc Tukey–Kramer tests. All statistical tests in this study were performed with the Statistics Toolbox in Matlab 7.0.1 (The Mathworks). Unless stated otherwise, all errors in this paper are reported as one SD.

Results

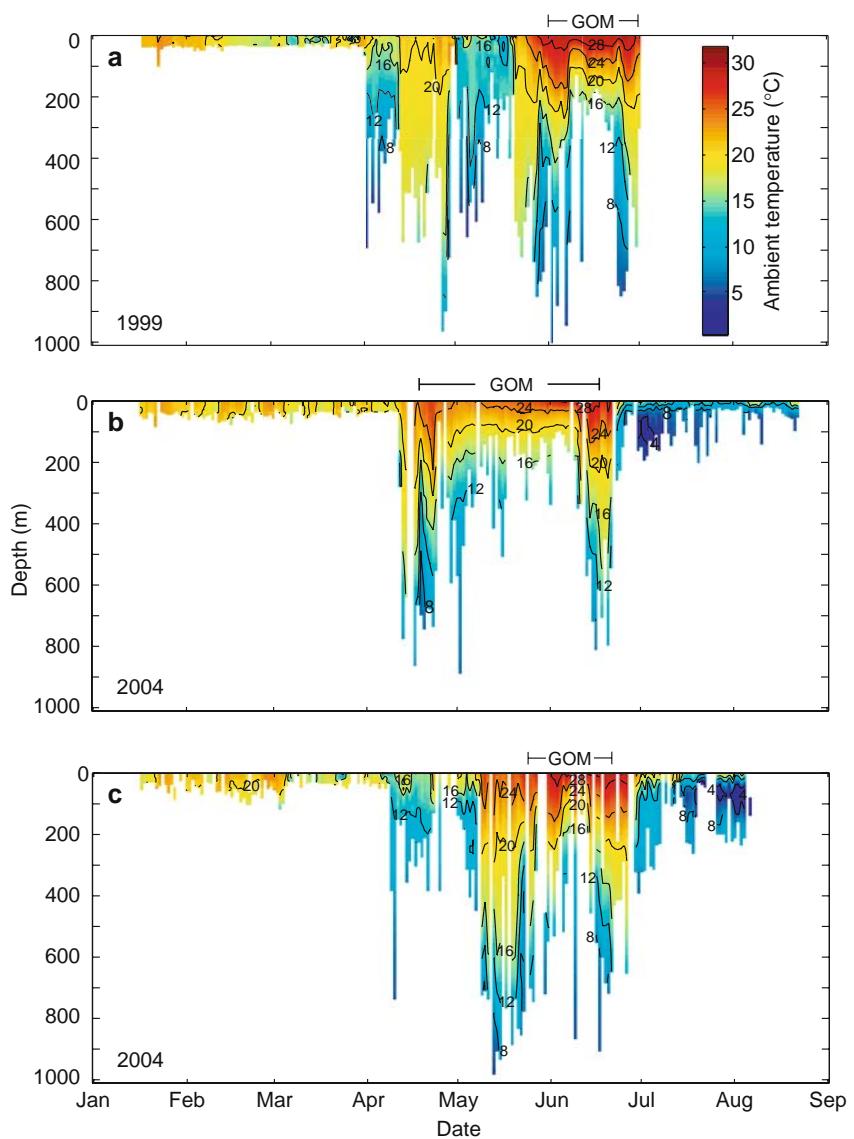
The movements of three representative Atlantic bluefin tuna (*T. thynnus*) that exhibited breeding migrations to the GOM are presented (Fig. 1). The bluefin tuna that entered the GOM during the breeding season were associated with feeding aggregations in North Carolina, mid-Atlantic Bight, and New England waters (Fig. 1). The fish entered the GOM from early February to early June and left the GOM by the end of June, staying in the GOM for an average of 39 ± 11 days. The bluefin tuna experienced the warmest sustained ambient temperatures of each track during the period in the GOM (Fig. 2). The SSTs experienced by the fish inside the GOM ($26.4 \pm 1.6^\circ\text{C}$) were significantly warmer ($P < 0.0001$, $\chi^2 = 19.9$, Kruskal–Wallis) than outside the GOM ($20.2 \pm 1.9^\circ\text{C}$, Fig. 3).

Diving behavior

The diving behavior of the Atlantic bluefin tuna in the GOM was delineated into three phases (entry, breed-

Fig. 2 *Thunnus thynnus*.

Daily ambient temperature–depth profiles of **a** bluefin 98–512, **b** bluefin 03–251 and **c** bluefin 03–230. Horizontal black lines indicate periods in the Gulf of Mexico



ing, and exit), as described above (Fig. 4). As the fish entered the GOM in the entry phase, they exhibited deep diving behavior during both the day and night (Figs. 4, 5). In contrast, during the putative breeding phase, the fish remained in relatively shallow depths and exhibited shallow, oscillatory dives at night (Figs. 4, 5). The mean daily maximum depths during the breeding period (203 ± 76 m) were significantly shallower ($P < 0.001$, Tukey–Kramer) than the entry (568 ± 50 m) and exit phases (580 ± 144 m, Fig. 6). The bluefin tuna were in the breeding phase for an average of 18 ± 7 days. After the breeding phase, the Atlantic bluefin began the exit phase and exhibited deep diving behavior similar to the entry phase (Figs. 4, 5). The daily maximum depths in the exit phase were not significantly different ($P > 0.05$, Tukey–Kramer) from the entry phase (Fig. 6).

During the putative breeding phase, the Atlantic bluefin tuna exhibited diel differences in diving behavior in May and June, but not in April. In April, the mean nighttime depths during the breeding phase were not significantly different ($P > 0.05$, $\chi^2 = 0.47$, Kruskal–Wallis) from the mean daytime depths (Table 2). However, the mean nighttime depths during the breeding phase were significantly shallower than daytime depths in May ($P < 0.01$, $\chi^2 = 7.93$, Kruskal–Wallis) and June ($P < 0.0001$, $\chi^2 = 31.46$, Kruskal–Wallis, Table 2).

Horizontal movements

Similar to the observed changes in diving behavior, the horizontal movement paths of the Atlantic bluefin tuna also changed between the entry, breeding, and exit

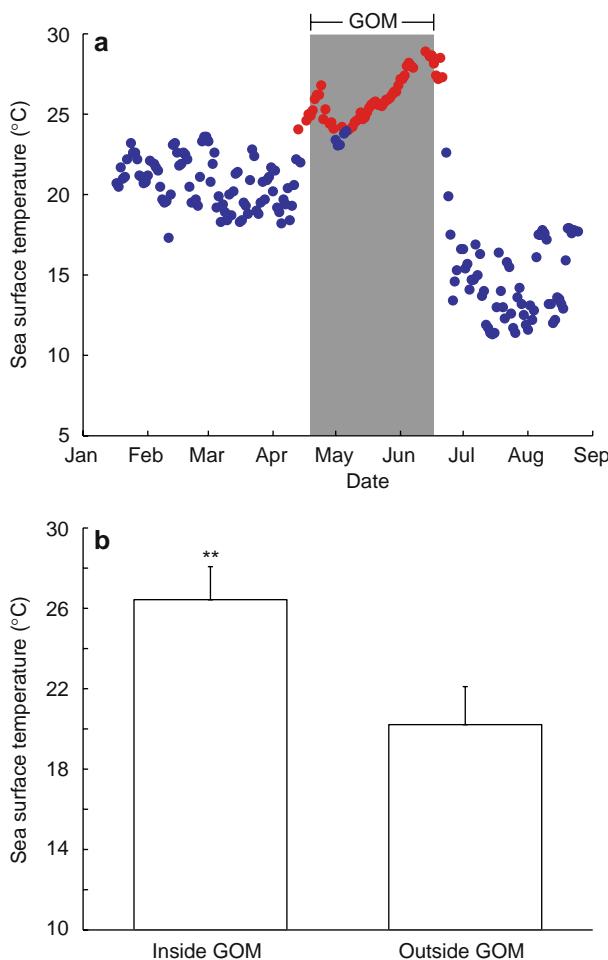


Fig. 3 *Thunnus thynnus*. **a** Mean daily sea surface temperature (SST) experienced by bluefin 03–251. Red circles indicate SSTs $\geq 24^{\circ}\text{C}$ and blue circles indicate SSTs $< 24^{\circ}\text{C}$. Period in the Gulf of Mexico (GOM) indicated by grey bar and horizontal black line. **b** SSTs experienced by Atlantic bluefin tuna ($n = 27$) inside and outside the GOM. **SSTs inside GOM were significantly warmer than outside ($P < 0.0001$). Error bars indicate 1 SD

phases. The MSD scores during the entry ($3.45 \pm 2.01 \times 10^4 \text{ km}^2$) and exit ($5.17 \pm 2.00 \times 10^4 \text{ km}^2$) phases were significantly higher ($P < 0.05$, Tukey–Kramer) than the MSD scores in the putative breeding phase ($0.60 \pm 0.41 \times 10^4 \text{ km}^2$, Fig. 7), indicating that the fish were significantly more residential during the breeding phase. Similarly, the LI scores during the deep diving entry (0.841 ± 0.074) and exit (0.905 ± 0.044) phases were significantly higher ($P < 0.05$, Tukey–Kramer) than the LI scores in the putative breeding phase (0.565 ± 0.131 , Fig. S1), indicating that the movement paths were significantly more linear during the entry and exit phases.

Ambient temperatures

There were also differences between the SSTs experienced by the fish in the entry, breeding, and exit

phases. The mean daily SSTs during the putative breeding phase ($25.8 \pm 1.5^{\circ}\text{C}$) were not significantly different ($P > 0.05$, Tukey–Kramer) from the entry phase ($27.1 \pm 1.6^{\circ}\text{C}$) but were significantly cooler ($P < 0.05$, Tukey–Kramer) than the exit phase ($27.4 \pm 1.5^{\circ}\text{C}$).

The diel differences in the ambient temperatures during the breeding phase varied by month. In April, the mean nighttime temperatures during the breeding phase were not significantly different ($P > 0.05$, $\chi^2 = 3.69$, Kruskal–Wallis) from the mean daytime temperatures (Table 2). However, the mean nighttime temperatures during the breeding phase were significantly warmer than the mean daytime temperatures in May ($P < 0.001$, $\chi^2 = 13.07$, Kruskal–Wallis) and June ($P < 0.0001$, $\chi^2 = 35.3$, Kruskal–Wallis, Table 2). In addition, the ambient temperatures during the breeding phase had a smaller range and variance (Fig. 5).

During the day, the mean depths exhibited by the Atlantic bluefin tuna in the breeding phase were significantly positively correlated ($P < 0.0001$, $R^2 = 0.32$) to the SSTs experienced by the fish (Fig. S2). The fish exhibited greater mean depths during the day as the SST increased. In contrast, the mean depths during the night were significantly negatively correlated ($P < 0.001$, $R^2 = 0.14$) to the SSTs experienced by the fish (Fig. S2).

Body temperature

Bluefin 98–512, which was identified as a female upon recapture, provided an archival tag record in the GOM with concurrent depth, ambient and body temperature data. This record provided an opportunity for the detailed analysis of the thermal biology of a breeding bluefin tuna in the GOM. In addition, bluefin 98–512 exhibited fidelity to the GOM spawning grounds, making two annual migrations to the GOM breeding grounds in 1999 and 2000 (Fig. 8), allowing us to compare the body temperature and depth data from two consecutive years (Fig. 9). Bluefin 98–512 was in the GOM during 2–28 June 1999 and from 24 April to 11 June 2000 (Fig. 8).

For both years, as bluefin 98–512 traveled from the foraging grounds in the North Atlantic Ocean to the breeding grounds in the GOM, there was a distinct, corresponding increase in body temperature (Fig. 9). In 1999, the daily mean body temperature increased rapidly ($0.37^{\circ}\text{C day}^{-1}$) as the fish migrated towards the GOM, with the daily mean body temperatures peaking at 29.0°C just before it entered the GOM (Fig. 9). In 2000, the daily mean body temperatures increased at $0.30^{\circ}\text{C day}^{-1}$ as the fish migrated towards the GOM.

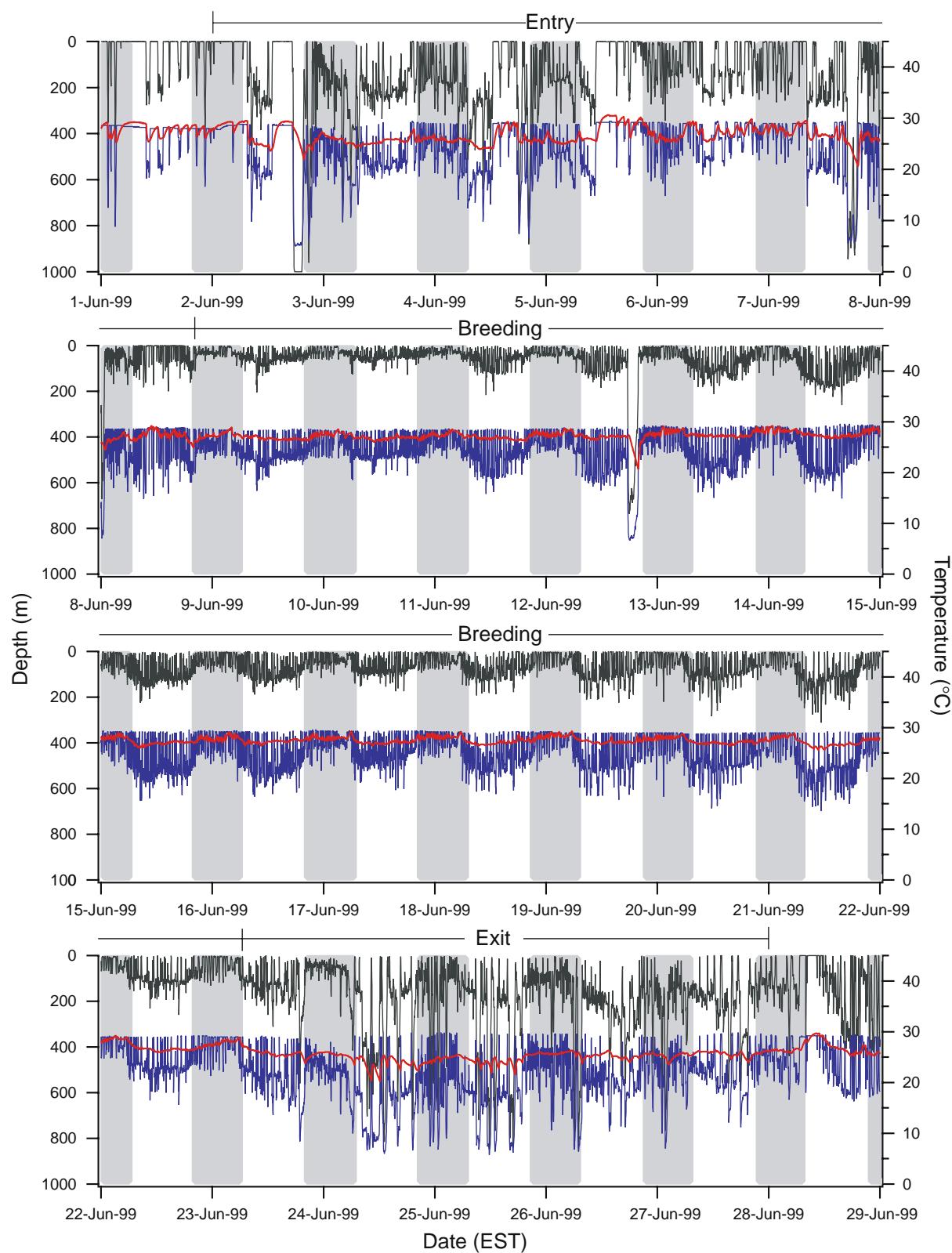


Fig. 4 *Thunnus thynnus*. Depth (black), ambient temperature (blue) and body temperature (red) of bluefin 98–512 in June 1999 (inside GOM). Vertical grey bars indicate nighttime. Horizontal black lines indicate entry, breeding, and exit phases

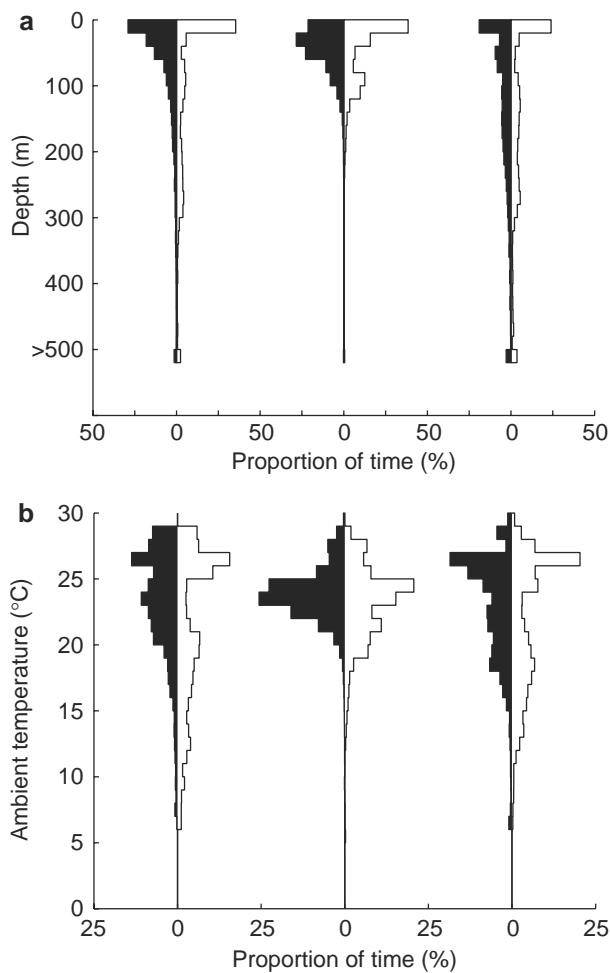


Fig. 5 *Thunnus thynnus*. **a** Depth and **b** ambient temperature distributions of Atlantic bluefin tuna ($n = 11$) in entry, breeding, and exit phases. White and black bars indicate day and night, respectively. Only fish tagged with archival or recovered PAT tags were included

The daily mean body temperatures peaked at 28.5°C , after it had entered the GOM (Fig. 9). Within the GOM, the body temperatures in 1999 ($26.8 \pm 1.4^{\circ}\text{C}$)

Table 2 *Thunnus thynnus*. Daily depths and ambient temperatures, by month, of Atlantic bluefin tuna (11) in the breeding phase, during day and night

Month	Depth (m)		Ambient temperature (°C)	
	Day	Night	Day	Night
April	54 ± 41	54 ± 28	22.6 ± 1.5	23.1 ± 1.0
May	61 ± 27	$40 \pm 14^{**}$	23.4 ± 1.1	$24.5 \pm 1.0^{**}$
June	77 ± 25	$29 \pm 11^{**}$	23.0 ± 0.8	$26.8 \pm 0.8^{**}$

Values are mean \pm SD. Only fish tagged with archival tags or recovered PAT tags were included analysis because transmitted PAT data do not include mean depths

**Indicates significant diel differences ($P < 0.01$) for that month

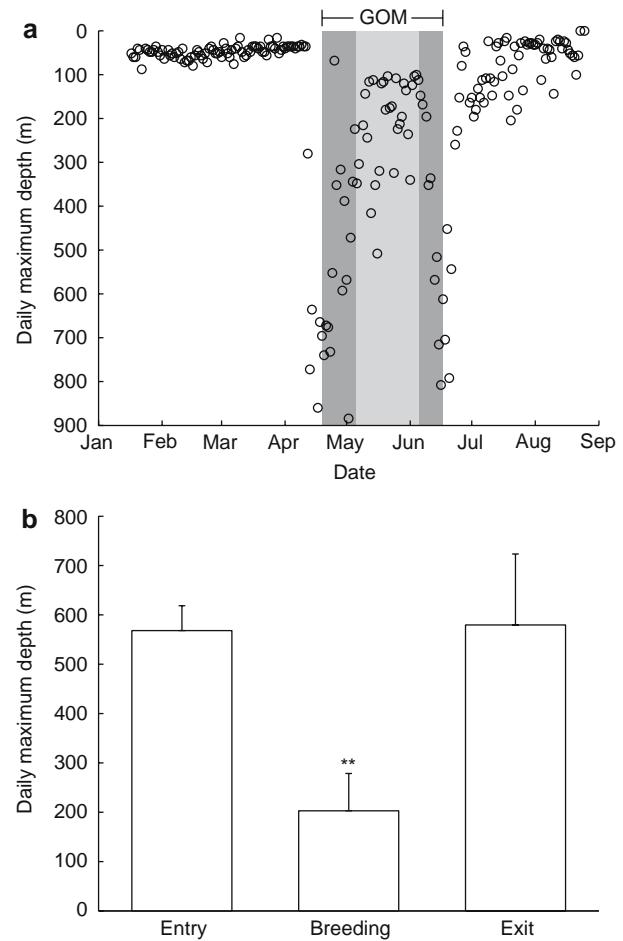


Fig. 6 *Thunnus thynnus*. **a** Daily maximum depths of bluefin 03–251. Horizontal black line indicates period in the Gulf of Mexico (GOM). Dark grey bar indicates entry and exit phases. Light grey bar indicates breeding phase. **b** Daily maximum depths of Atlantic bluefin tuna ($n = 28$) in entry, breeding, and exit phases. **Breeding phase maximum depths were significantly shallower than entry and exit phases ($P < 0.001$, Tukey–Kramer test). Error bars indicate 1 SD

were significantly warmer ($P < 0.0001$, $\chi^2 = 5,558$, Kruskal–Wallis) than in 2000 ($26.0 \pm 1.3^{\circ}\text{C}$). The changes in body temperature were significantly correlated ($P < 0.0001$, $R^2 = 0.734$) to the changes in the ambient temperature experienced by the bluefin tuna in the GOM in 1999 (Fig. 9).

Combining both periods in the GOM (1999 and 2000), the mean body temperature within the GOM ($26.7 \pm 1.6^{\circ}\text{C}$) was significantly warmer ($P < 0.001$, $\chi^2 = 4,076$, Kruskal–Wallis) than when the fish was outside the GOM ($24.7 \pm 2.3^{\circ}\text{C}$). However, there were interannual differences in the body temperature during the breeding phase. In 1999, the night body temperatures from the breeding phase were significantly warmer ($P < 0.05$, Tukey–Kramer) than the day (Table 3, Fig. S3). In addition, the night breeding phase body

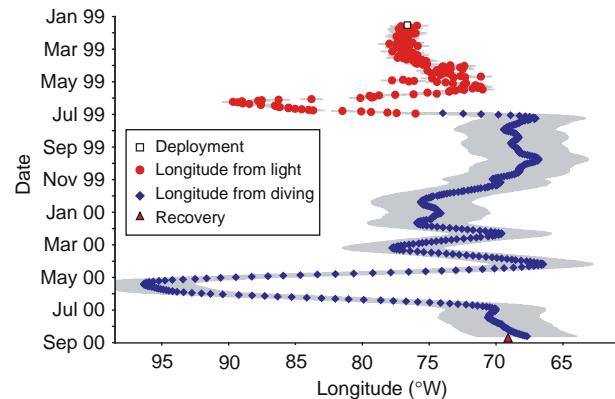
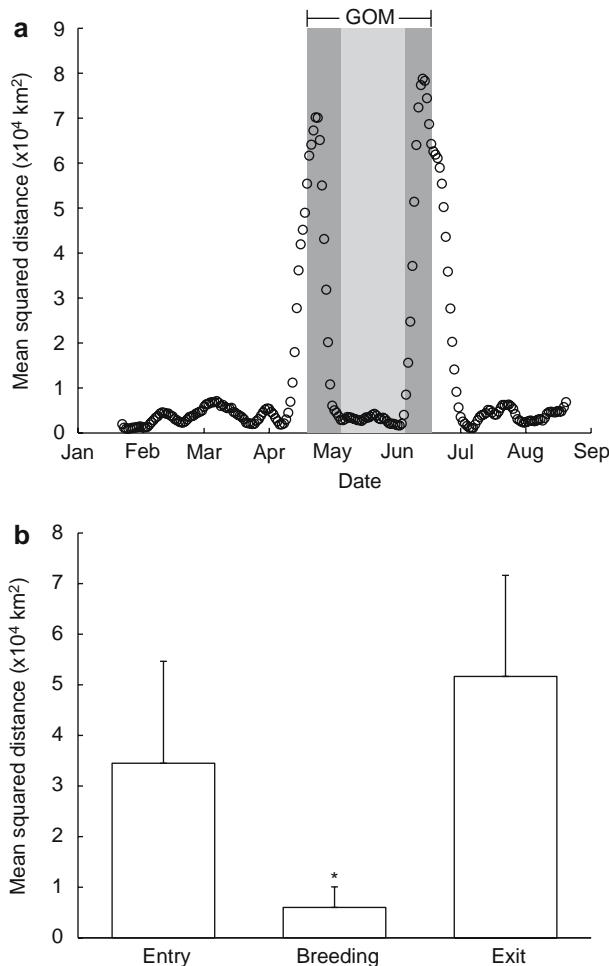


Fig. 8 *Thunnus thynnus*. Longitude estimates of bluefin 98–512 from light level data (red circles, 17 January 1999–2 July 1999), and from sunrise and sunset diving behavior (blue diamonds, 3 July 1999–21 August 2000). Horizontal grey bars indicate root mean square errors of longitude estimates

the fish during the putative breeding phase, which resulted in the fish experiencing warmer ambient and body temperatures. During the breeding phase, the K was significantly higher at night ($P < 0.001$, Tukey–Kramer) than the day (Fig. 10; Table 3). There were no significant diel differences in the K during the entry and exit phases ($P > 0.05$, Tukey–Kramer, Table 3). During the night of the breeding phase, bluefin 98–512 spent 29% of its time in the mixed layer (10 m, Fig. 10), which resulted in the fish experiencing significantly warmer ambient temperatures ($P < 0.05$, Tukey–Kramer, Table 3). The warmer ambient temperatures would in turn result in higher K values because K changed in relation to changing ambient and body temperatures (Fig. 11). The K of bluefin 98–512 was small at low ambient and body temperatures but increased rapidly at high temperatures (Fig. 11).

Bluefin tuna A0532 also exhibited fidelity to the GOM spawning grounds, making three annual migrations to the GOM breeding grounds from 2003 to 2005 (Fig. S4). This allowed us to compare the ambient and body temperature, and depth data from three consecutive years (Fig. 12). The depth and thermal patterns of bluefin A0532 appeared similar to bluefin 98–512. For all three years, the body temperatures during the breeding phases were significantly warmer (2003, $27.1 \pm 0.7^\circ\text{C}$, $P < 0.05$; 2004, $26.7 \pm 0.6^\circ\text{C}$, $P < 0.05$; 2005, $26.5 \pm 0.5^\circ\text{C}$, $P < 0.05$; Tukey–Kramer) than the entry and exit phases. This was likely related to the shallow diving and warm ambient temperatures during the breeding phase (Fig. S5). Bluefin A0532 also exhibited similar shallow oscillatory diving during breeding phase nights for all three years (Fig. 12).

temperatures were also significantly warmer ($P < 0.05$, Tukey–Kramer) than both the day and night body temperatures from the entry and exit phases (Table 3). In contrast, the night body temperatures during the breeding phase in 2000 were not significantly different ($P > 0.05$, Tukey–Kramer) from the day (Table 3, Fig. S3). However, both the day and night body temperatures during the breeding phase in 2000 were significantly warmer ($P < 0.05$, Tukey–Kramer) than the day and night body temperatures from the entry and exit phases (Table 3).

There were large diel differences in the whole body heat transfer coefficient, K , of bluefin 98–512 during the breeding phase in 1999. These diel differences were most likely related to changes in the diving behavior of

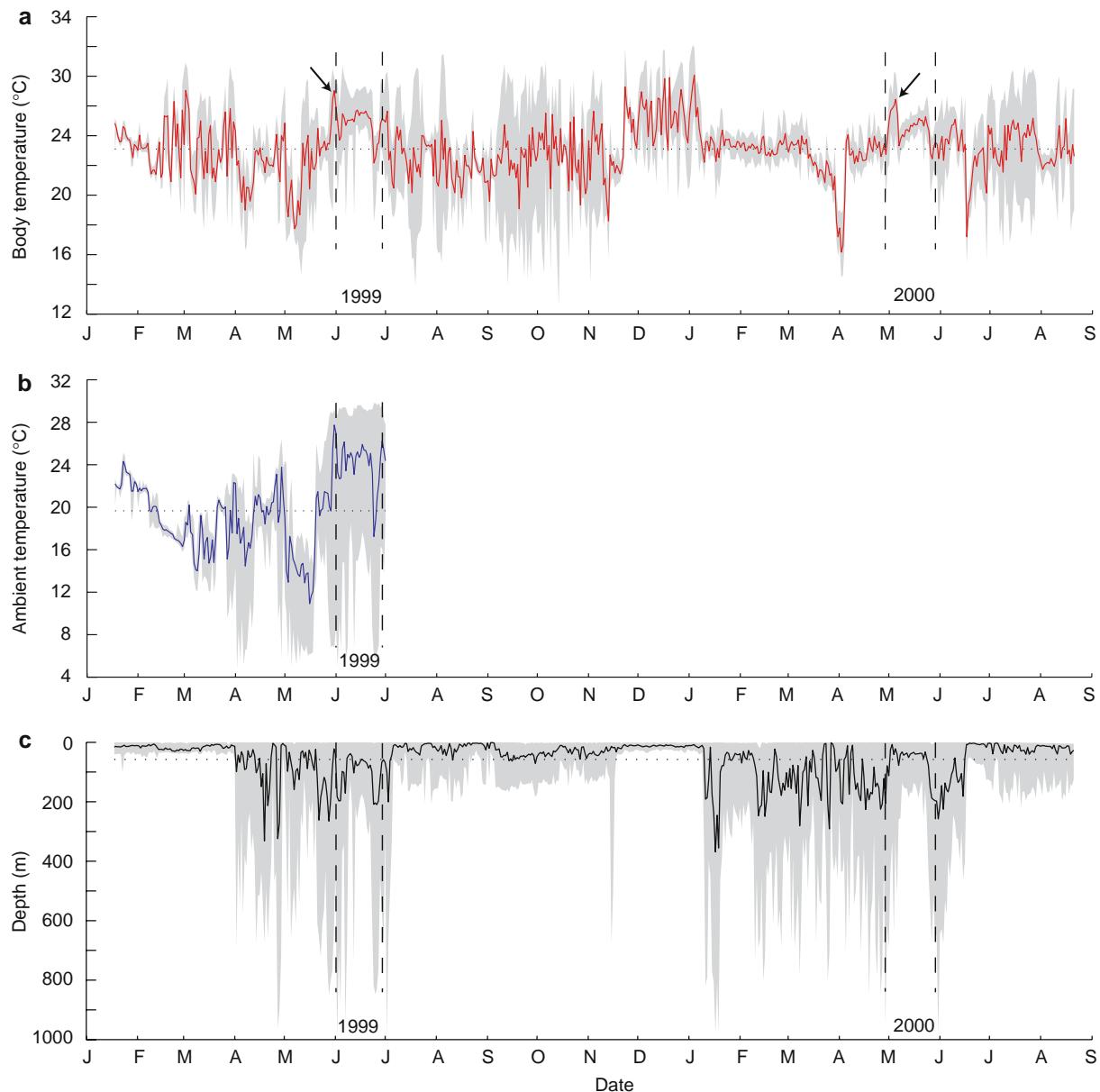


Fig. 9 *Thunnus thynnus*. Daily mean **a** body temperature, **b** ambient temperature and **c** depth of bluefin 98–512 (archival tag). Grey areas indicate daily range of temperatures and depths (minimum to maximum). Vertical dashed lines indicate periods in

the Gulf of Mexico. Arrows indicate peak of body temperatures recorded on breeding migrations from the North Atlantic into the GOM. Ambient temperature data ends on 2 July 1999 when external sensors failed

Discussion

We used electronic tags to discern the distinct diving behaviors, horizontal movements, and thermal biology of Atlantic bluefin tuna (*T. thynnus*) on their breeding grounds in the GOM and defined the entry, breeding, and exit phases from the electronic tag data.

The entry and exit phases were characterized by deep diving and rapid, directed movement paths into and out of the GOM. The deep diving during the entry and exit phases most likely represents an attempt to

thermoregulate or reduce the energetic cost of swimming against the Loop Current. The deep diving would allow the fish to avoid the Loop Current, which is very warm and rapidly advects out of the GOM. Importantly, the reduced cost of locomotion from deep diving would only apply to the entry phase because it would likely be energetically cheaper to swim within the Loop Current during the exit phase. Therefore, the deep diving in the exit phase suggests that this behavior is, at least in part, an attempt to avoid the warm surface waters and thermoregulate. However, we cannot rule

Table 3 *Thunnus thynnus*. Mean depths, ambient water temperatures (Ta), body temperatures (Tb), and whole body heat transfer coefficients (K) of bluefin 98–512 during night and day of entry, breeding, and exit phases in the Gulf of Mexico

	Entry		Breeding		Exit	
	Day	Night	Day	Night	Day	Night
Depth (m)	147 ± 184	114 ± 127	84 ± 72	31 ± 25*	224 ± 158	119 ± 110
Ta (°C)	23.7 ± 5.5	25.1 ± 4.2	23.5 ± 3.6	27.3 ± 1.8*	18.8 ± 5.5	23.2 ± 4.5
Tb (°C)	26.8 ± 1.7	26.7 ± 1.3	27.1 ± 0.7	27.9 ± 0.5*	25.0 ± 1.2	25.6 ± 1.0
K (10^{-4} s $^{-1}$)	2.3 ± 2.4	2.5 ± 2.3	0.98 ± 1.3	5.4 ± 2.7*	0.7 ± 0.63	0.7 ± 0.8
1999						
Depth (m)	190 ± 129	103 ± 121	68 ± 104	44 ± 81*	194 ± 129	93 ± 103
Tb (°C)	25.0 ± 0.8	25.2 ± 0.7	26.6 ± 1.2 ^a	26.5 ± 1.2 ^a	25.4 ± 1.4	26.2 ± 1.0
2000 ^b						

^a Indicates Tb during day and night of breeding period in 2000 were significantly different ($P < 0.05$, Tukey-Kramer) from other four periods

^b Only body temperature and depth data were available in 2000 because external sensors for bluefin 98–512 failed on 2 July 1999

*Indicates mean depth, Ta, Tb, and K during the night of breeding period were significantly different ($P < 0.05$, Tukey-Kramer) from other five periods

out other possible explanations like avoidance of predators near the surface or foraging for prey, such as squid in the deep ocean.

The Atlantic bluefin tuna exhibited directed movement paths with high MSD and LI scores during the entry and exit phases but switched to highly sinuous movement paths with low MSD and LI scores during the breeding phase. These changes in the MSD and LI scores indicate that the bluefin tuna exhibited relatively linear, directed movement paths during the entry and exit phases but were relatively resident during the breeding phase. This is consistent with the fish exhibiting periods of rapid migration to and from the spawning areas but becoming relatively resident once they reach the spawning area (Prince et al. 2005). The bluefin tuna may be using environmental cues such as water temperature and clarity to determine the timing and location of spawning. However, more work needs to be done to determine what these cues are and how the bluefin tuna respond to these environmental signals.

The breeding phase is sandwiched between the entry and exit phases and can be identified from distinctive changes in the diving behavior, horizontal movements, and thermal biology. Since we did not directly observe the release of eggs and sperm into the water by the tagged bluefin tuna, we do not have direct proof that the fish were spawning during the breeding phase. However, the gonads of bluefin tuna that were caught on longlines in the same season and area, were examined using histological techniques and identified to be in spawning condition (Block et al. 2005). In addition, relatively high concentrations of bluefin tuna larvae have been caught in the same region at the same time of year (Richards et al. 1989; Tsuji et al. 1995; Nishida

et al. 1998). We also show that the Atlantic bluefin tuna changed their diving behavior and movement paths during the breeding phase, which we hypothesize to be indicative of courtship and/or spawning behavior. During the night in the breeding phase, the bluefin tuna exhibited shallow diving behavior, which was accompanied by frequent visits to the surface. This behavior, which may be courtship or spawning behavior, is in concordance with estimates of spawning times for other species of tunas in the wild (McPherson 1991; Nikaido et al. 1991; Schaefer 1996, 1998) and captive populations of spawning Pacific bluefin tunas (S. Masa-suma, Japan Sea Farming Association, personal communication) and yellowfin tuna (Schaefer 2001). The shallow diving during the breeding phase is not likely due to the fish being restricted by the bathymetry of the location because the breeding phase locations were primarily on the continental slopes of the northern GOM (Teo 2006). In addition, acoustic tracking of Pacific bluefin tuna indicate that the fish exhibit similar diving behavior on their breeding grounds in the East China Sea (NRIFSF 2002; Kitagawa et al. 2006).

The changes in diving behavior during the breeding phase were accompanied by changes in their thermal biology. Due to the shallower diving in the breeding phase, the fish experienced warmer ambient and body temperature distributions. The shallow diving behavior was more pronounced at night, leading to substantially warmer night ambient and body temperatures (Table 3). The high ambient temperatures in the night led to a fivefold increase in the heat transfer coefficient, K , as compared to the day because K increases rapidly at high temperatures. The fish exhibited distinct changes in their diving behavior and horizontal movements during the breeding phase, and experience distinct

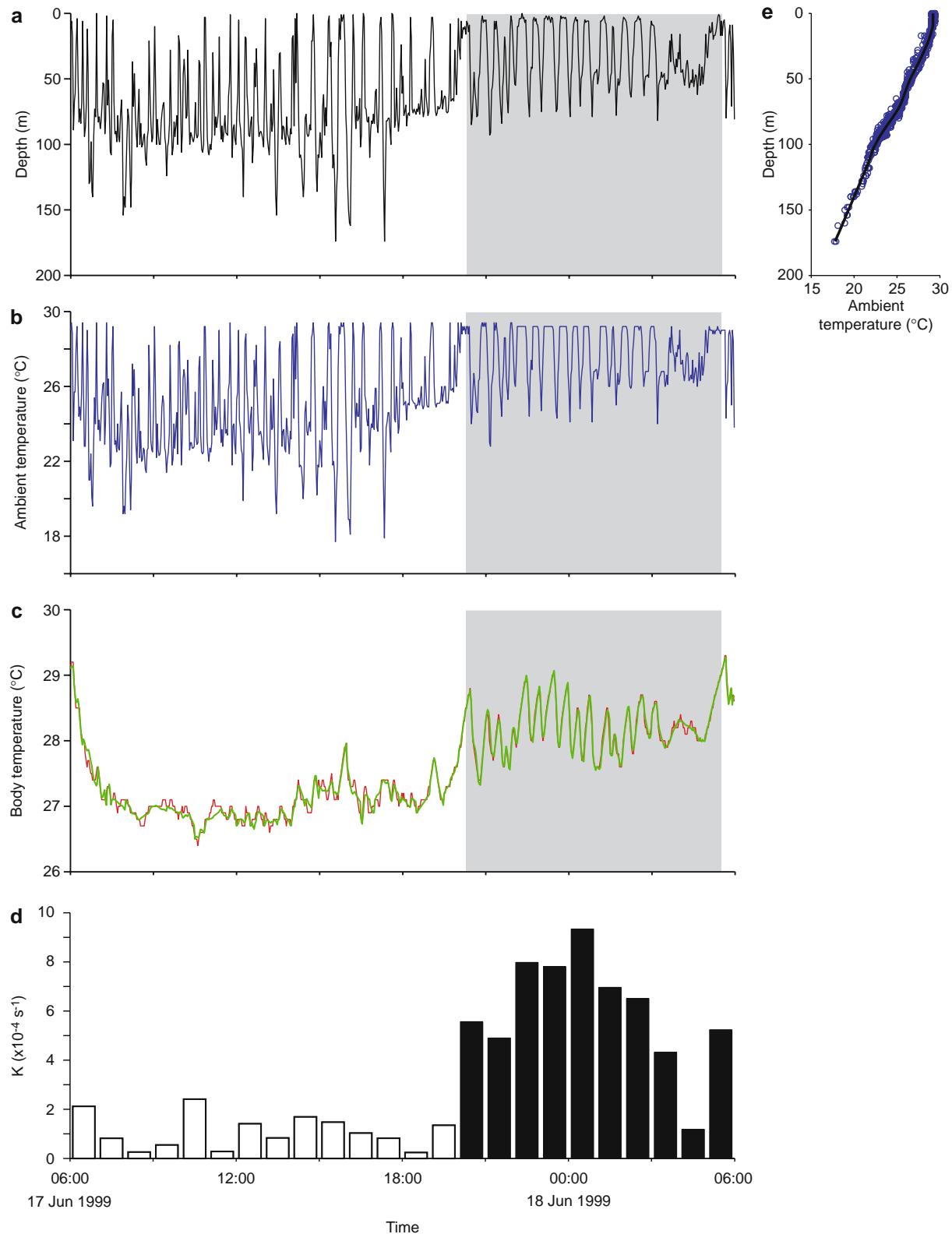


Fig. 10 *Thunnus thynnus*. Time-series of bluefin 98–512 during a 24 h period (17–18 June 1999) in the breeding phase, **a** depth and **b**, ambient temperature, **c** correspondence of modeled (green) to measured body temperature (red). Grey bars indicate nighttime.

d Hourly heat transfer coefficient (K). White and black bars indicate day and night, respectively. **e** Temperature profile of water mass. Black line indicate best loess fit line

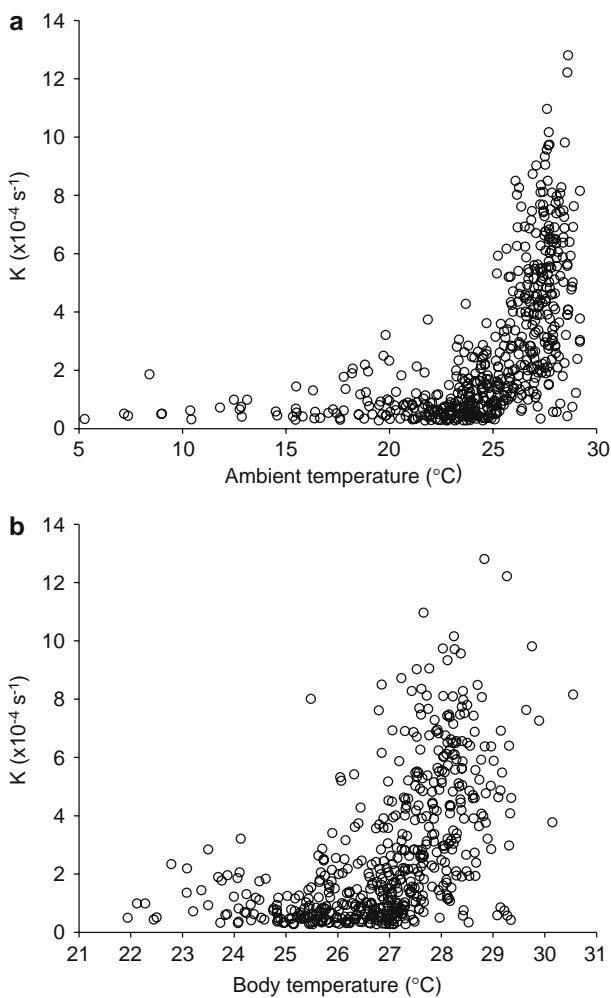


Fig. 11 *Thunnus thynnus*. Relationship between heat transfer coefficient, K , and **a** mean ambient and **b** body temperatures of bluefin 98–512, in the Gulf of Mexico ($n = 504$)

changes in their thermal biology. This suggests that we can use these as potential signals of the breeding phase of Atlantic bluefin tuna in the GOM. These signals can be used in future studies to elucidate the location and timing of breeding in the GOM, in relation to the environment.

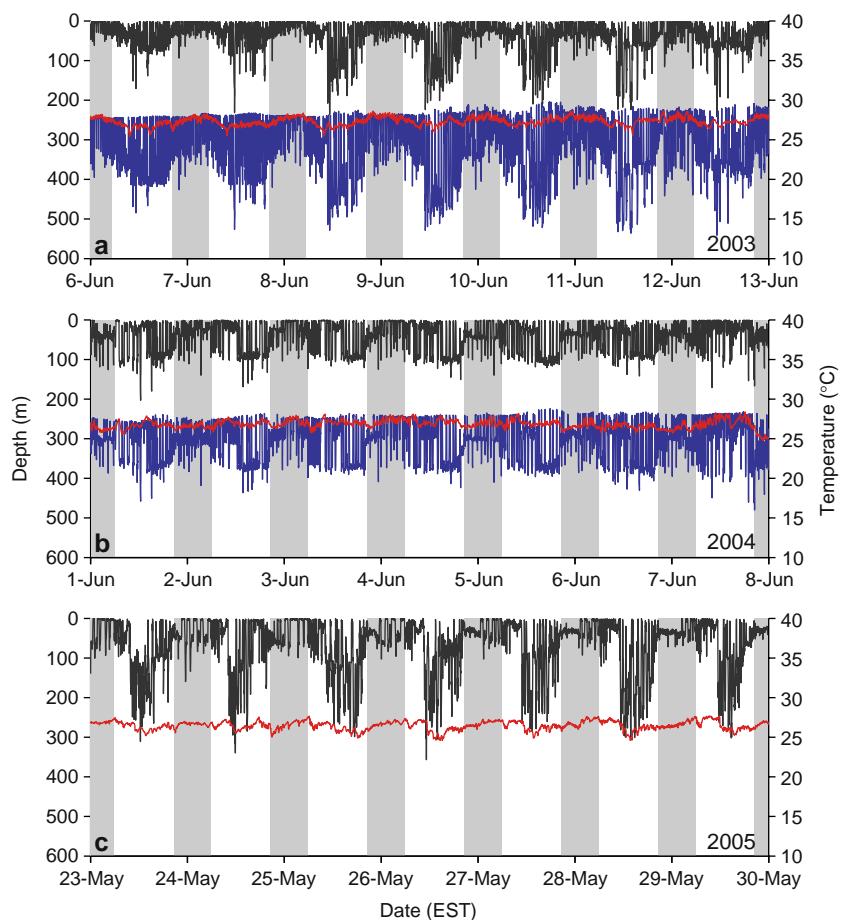
The interaction between T_a , T_b , and K of the Atlantic bluefin tuna plays an important role in the thermal biology during the breeding migration. We demonstrate that the Atlantic bluefin tuna have the capacity to increase K at the high T_a and T_b encountered in the GOM. Giant Atlantic bluefin tuna have previously been shown, with acoustic telemetry and muscle temperature measurements, to maintain a low K ($0.23\text{--}0.33 \times 10^{-4} \text{ s}^{-1}$) for heat conservation in the cool waters of the foraging grounds (Carey and Lawson 1973; Neill and Stevens 1974). However, the increase in K at the high ambient and body temperatures

encountered on the breeding grounds has not been observed previously. The increases in K are likely due to vasodilation and/or an increase in cardiac output, since tuna hearts function at close to ambient temperatures and the vascular systems of bluefin tunas do not have a clear vascular route that bypasses the heat exchanger (Bushnell and Jones 1994; Graham and Dickson 2001). Laboratory studies have shown that the cardiac outputs of Pacific bluefin and yellowfin tuna increase as a function of ambient temperature, with a Q_{10} effect of ~2 (Korsmeyer et al. 1997; Blank et al. 2002, 2004). This increase in cardiac output would result in an increase in K and hence convective cooling. However, this increase in cardiac output at high temperatures is not likely to account for the entire increase in K because K increases sharply after the ambient temperature reaches approximately 25–26°C. This sharp increase in K may in part be due to a phase shift in the thermal biology, where reduction of heat content becomes a high priority. We hypothesize that, at the high temperatures in the GOM, the Atlantic bluefin tuna may no longer need a low K for heat conservation, and may be depending more on changes in diving behavior for thermoregulation. In this situation, having a high K by dilating blood vessels would be advantageous because blood flow to the gills would increase and its body temperature would be closer to ambient temperature.

The K from bluefin tuna on their breeding grounds were higher than the previously reported K for similar-sized bluefin tuna in the cool waters of the foraging grounds (Carey and Lawson 1973; Neill and Stevens 1974). The difference in K between the studies is likely due to the warmer ambient temperatures in the GOM and the different placement of the tags. Carey and Lawson (1973) placed the tags into the muscle and stomach of the fish while we surgically implanted the tag into the peritoneal cavity. Thus our location of the tag is more peripheral than the placement from Carey and Lawson (1973), which would lead to higher K values. In addition, the K during the night of the breeding phase were in the range exhibited by juvenile Pacific bluefin tuna ($2.16\text{--}6.01 \times 10^{-4} \text{ s}^{-1}$, 45–78 cm fork length), which were tagged with archival tags on their feeding grounds (Kitagawa et al. 2001). However, the different sizes of the fish between the two studies make comparison difficult.

Yellowfin and bigeye tuna have been shown to thermoregulate by altering K and changing dive patterns, in response to changing T_a and T_b (Holland et al. 1992; Dewar et al. 1994). In bigeye tuna, the K is high when the T_a exceeds T_b and is low when the vice versa occurs (Holland et al. 1992). This enables the

Fig. 12 *Thunnus thynnus*. Bluefin A0532 visited the Gulf of Mexico for three consecutive years and exhibited breeding phase behavior. Depth (black), ambient temperature (blue) and body temperature (red) of bluefin A0532 during breeding phases in **a** 2003, **b** 2004, and **c** 2005. Vertical gray bars indicate nighttime. Ambient temperature data ends on 21 June 2004 when external sensors failed



bigeye tuna to raise T_b when the fish is in warm surface waters but conserve heat when the fish is diving to cool waters at depth. However, the role of the change in K for breeding bluefin tuna is probably not the same as that for diving bigeye tuna because the K did not change substantially between the ascending and descending portions of each dive. In addition, the difference in the changes in K may also be due to the differences in the vascular system between the species, where bluefin tuna appear to be less able to bypass the heat exchanger system (Graham and Dickson 2001).

The thermal biology of giant bluefin tuna at the high temperatures experienced in the GOM may help explain why the bluefin tuna experience relatively high mortality on longlines in the GOM (Block et al. 2005). Block et al. (2005) observed that giant Atlantic bluefin tuna caught on scientific longlines in the GOM suffered from relatively high mortality (up to 1.38 bluefin tuna per 1,000 hook hours). If the giant bluefin tuna were caught in warm surface waters and were unable to dive below the mixed layer to thermoregulate, they may have become stressed from the high temperatures in addition to the sympathetic stress of capture. This may have resulted in the bluefin tuna suffering a higher

mortality from longlines in the GOM than when the fish are caught on longlines in cooler waters. In addition, it would also be important to determine if and how the changes in K are related to body size (Kitagawa et al. 2006).

In the future, it would be important to determine if the high oxygen requirements of Atlantic bluefin tuna affect its diving behavior and thermal biology on the breeding grounds. Based on CTD casts during scientific longline cruises from 1999 to 2002 (Block et al. 2005), the surface oxygen content of the breeding areas during the breeding season ranged from 4.6 to 5.3 mg l⁻¹ (Fig. S6). Since courtship and spawning behaviors can lead to higher metabolic rates in fish (Macey et al. 1991), this may lead to increased metabolic stress. In addition, laboratory experiments on Pacific bluefin tuna indicate that metabolic rate increases considerably with increasing ambient temperature (Blank 2006). Therefore, more work needs to be done to determine the metabolic rates of Atlantic bluefin tuna at high temperatures and if the oxygen content in the water column is affecting their diving behavior.

Based on longline observer data, Atlantic bluefin tuna are in the GOM from December to June (Block

et al. 2005; Teo 2006). In this study, most of the bluefin tuna entered the GOM in April–June. One fish entered the GOM in February but the tag did not return any GOM data for analysis. It would therefore be important, in the future, to obtain data from bluefin tuna that enter the GOM in the winter months to see if their biology and body size is different from the fish examined in this study. The bluefin tuna occupying the GOM during the spawning season are extremely large in body size, with the mean size of electronically tagged bluefin tuna entering the GOM being 241 ± 28 cm CFL (Block et al. 2005). The size frequency distribution of bluefin tuna caught by the U.S. pelagic longline fleet in the GOM have also been reported previously to be very large, with a mode of 251–300 kg (Nemerson et al. 2000). This suggests that the median age to sexual maturity for the western stock of Atlantic bluefin tuna is closer to 11–12 year than the 8 year (assumed first age to maturity) currently being used in ICCAT assessment models. The use of electronic tagging data to examine the biology of breeding Atlantic bluefin tuna has provided managers with new information on the areas of aggregation, the timing of breeding and the size of fish at spawning. These data will improve our understanding of the spawning bluefin tuna in the western Atlantic and should be used to ensure their future.

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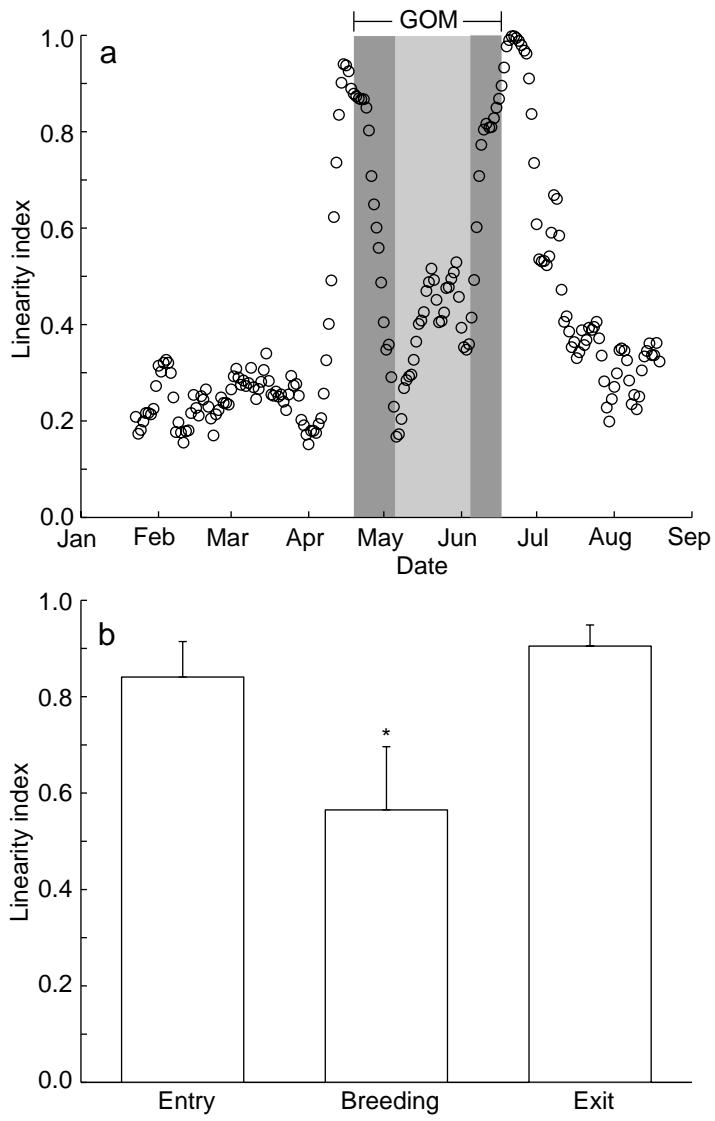


Fig. S1 *Thunnus thynnus*. **a** Linearity index (LI) scores of horizontal movement paths of bluefin 03-251. Horizontal black line indicates period in Gulf of Mexico (GOM). Dark gray bars indicate entry and exit phases. Light gray bar indicate breeding phase. **b** LI scores of Atlantic bluefin tuna ($n = 14$) during the entry, breeding, and exit phases.
 * Breeding phase LI scores were significantly lower than entry and exit phases ($p < 0.05$, Tukey-Kramer test). Error bars indicate one SD

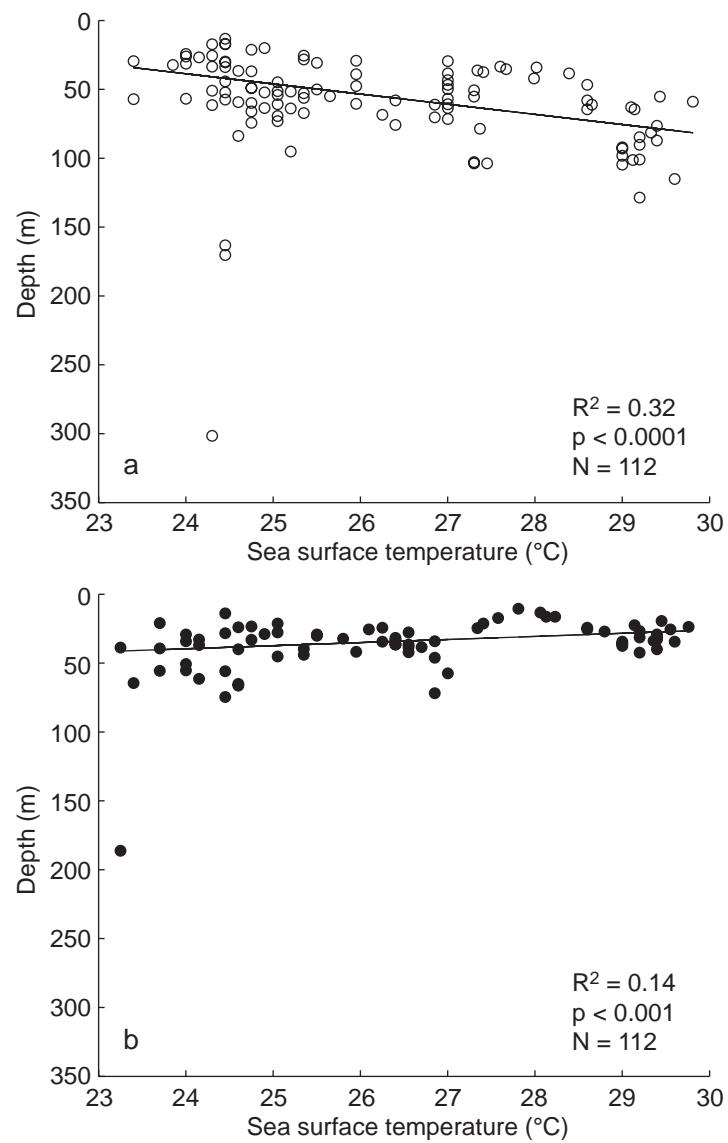


Fig. S2 *Thunnus thynnus*. Relationship between mean **a**, daytime (open circles) and **b**, nighttime (closed circles) depths exhibited by breeding phase Atlantic bluefin tuna and sea surface temperature. Black lines indicate robust linear fits

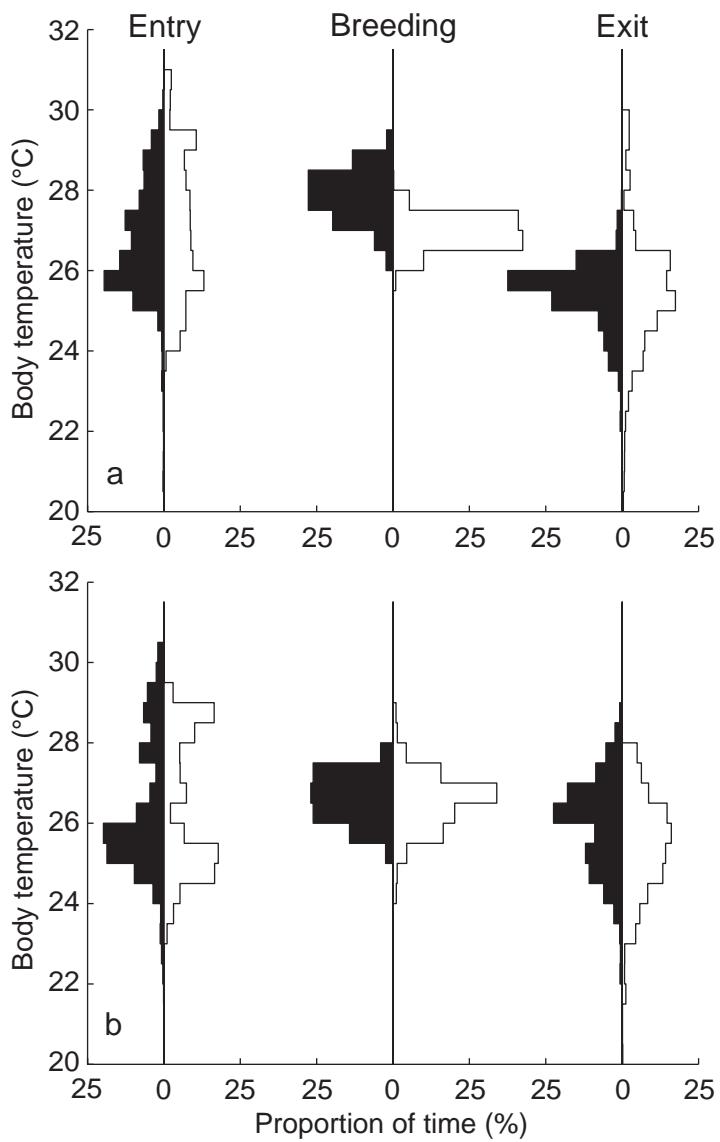


Fig. S3 *Thunnus thynnus*. Body temperature distributions of bluefin 98-512 during entry, breeding, and exit phases in a, 1999 and b, 2000. White and black bars indicate day and night, respectively

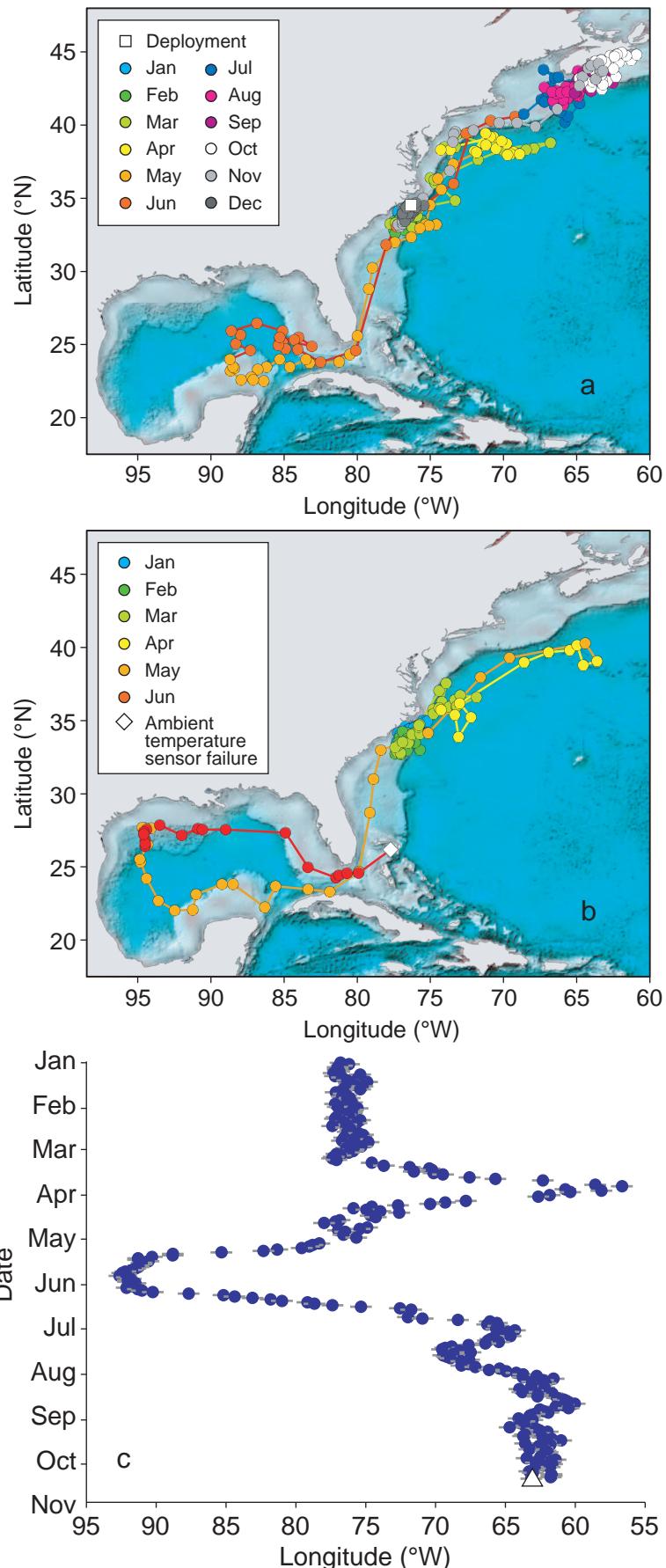


Fig. S4 *Thunnus thynnus*. Track of bluefin A0532 in **a**, 2003 and **b**, 2004. Archival tagged on 25 Jan 2003. Ambient temperature sensor failed on 21 June 2004. **c** Light level longitude estimates of bluefin A0532 in 2005. Recapture longitude (white triangle) is indicated. Horizontal gray bars indicate root mean square error for longitude estimates

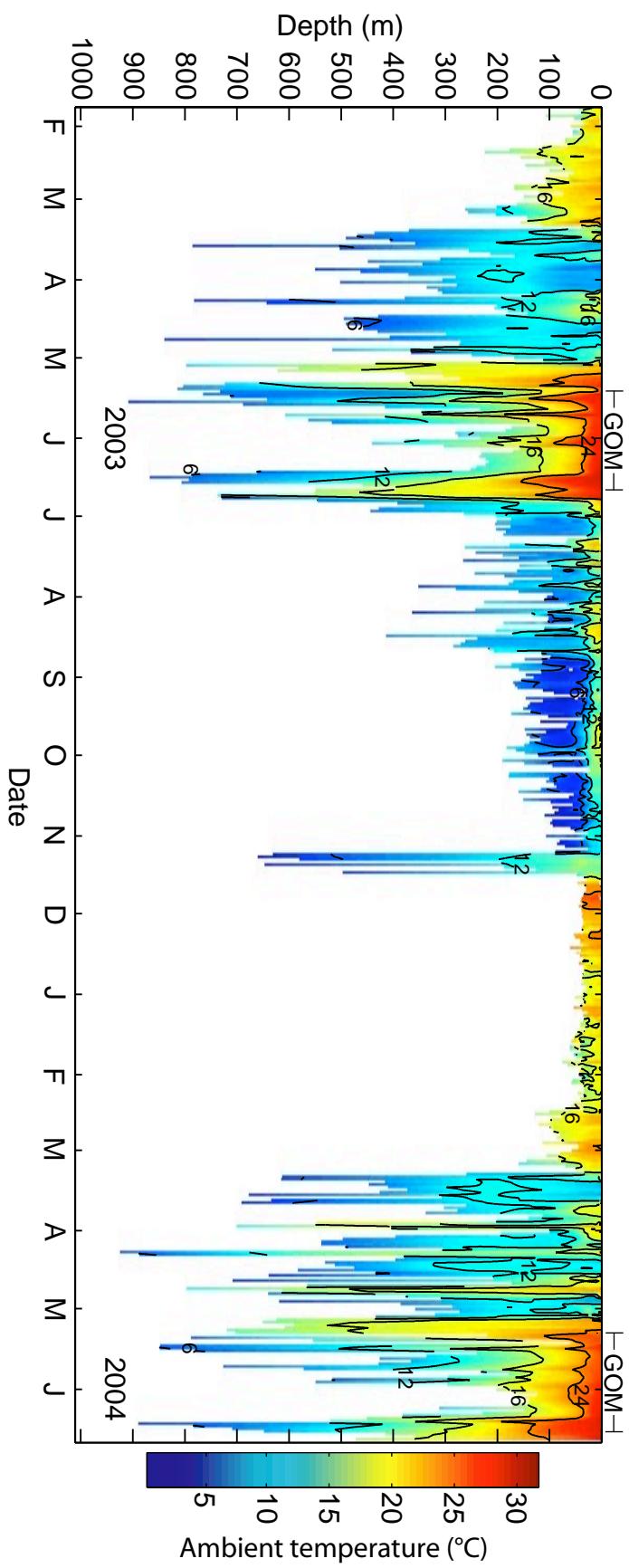


Fig. S5 *Thunnus thynnus*. Ambient temperature-depth profiles of bluefin A0532. Horizontal black lines indicate periods in the Gulf of Mexico. Ambient temperature sensor failed on 21 June 2004

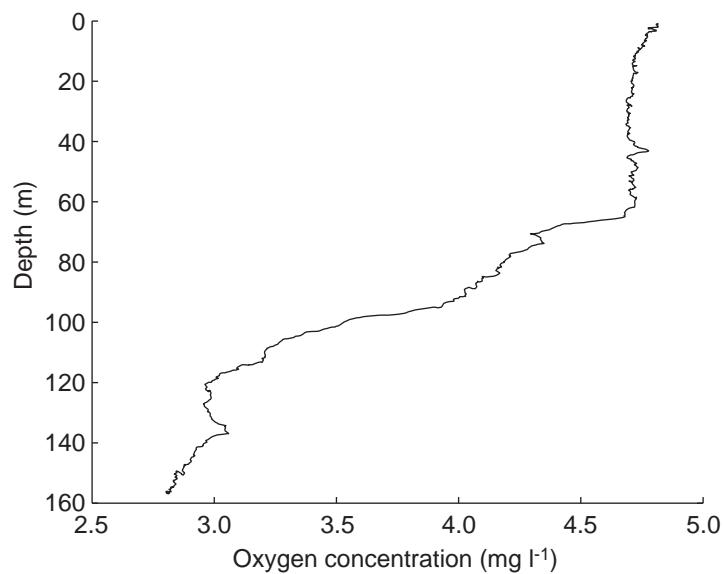


Fig. S6. Oxygen profile of breeding grounds in the Gulf of Mexico (27.233 °N, 91.798 °W; 11 April 2002). Oxygen profile was obtained using a CTD profiler (SBE19 plus SEACAT Profiler, Seabird Electronics), which was deployed on a scientific longline cruise in the Gulf of Mexico during the breeding season