Modeling swordfish daytime vertical habitat in the North Pacific Ocean from pop-up archival tags

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ABSTRACT: The daytime foraging depth of swordfish in the North Pacific was investigated with data from an 8 yr tagging program, using 28 Wildlife Computer pop-up archival tags deployed on swordfish in the North Pacific. The tags transmitted data from 1°S to 44°N latitude and from 206 to 249°E longitude. Five tags were recovered, providing a full archival record that showed that when swordfish did not engage in daytime basking behavior, they remained within a narrow range of light level during both day and night, suggesting swordfish stay within a sound-scattering layer (SSL) to feed during both day and night. Daytime mean depth of non-basking swordfish ranged from 32 to 760 m. Seventy-seven percent of the daytime mean depth could be explained with a generalized additive model that used 3 environmental indices: satellite-derived surface chlorophyll as a proxy for light at depth, oxygen at 400 m obtained from the World Ocean Atlas, and temperature at 400 m inferred from the tag data. This model, when used in a predictive mode, generated a basin-wide map of swordfish daytime mean depth that showed depths exceeding 600 m to the north of Hawaii, shoaling to 300 m off the coast of California. This information could improve daytime swordfish catch by longliners and potentially allow them to switch from shallow night sets that result in interactions with sea turtles. This approach in effect defines the habitat of swordfish prey, giving us insight into the vertical behavior of those mid-trophic level organisms inhabiting the SSL. Our model could be easily applied to other deep-foraging species.

KEY WORDS: *Xiphias gladius* · Swordfish · Satellite tracking · Generalized additive model · Habitat modelling

INTRODUCTION

The swordfish *Xiphias gladius* is a globally distributed, highly migratory species of billfish whose habitat in the Pacific Ocean ranges from 50°S to 50°N and from the surface to depths >1000 m. Swordfish support important commercial fisheries in all ocean basins as well as the Mediterranean Sea, most of which use shallow-set longlines. In 2008, more than 94 000 t of swordfish were harvested world-wide, with 40% of the catch from the Pacific Ocean (www.fao.org/fishery/statistics/global-capture-production/en, accessed Feb 10, 2011). The 2 main gear types used to target swordfish in the North Pacific are shallow-set longlines and drift gillnets. Using either gear type, swordfish are typically targeted at night in the upper part of the water column. Unfortunately, the near-surface waters are where the overlap between swordfish and non-target species is the greatest. As a result, swordfish fisheries have been

the focus of dramatic management actions to reduce bycatch, most notably because of their interactions with loggerhead *Caretta caretta* and leatherback *Dermochelys coriacea* sea turtles. Both of these species are considered to be endangered in most oceans (Lewison et al. 2004, Garcia-Cortes & Mejuto 2005, Watson et al. 2005, Baez et al. 2007, Gilman et al. 2007, Petersen et al. 2009, Piovano et al. 2009). Loggerhead turtles were relisted as endangered in the North and South Pacific by the National Marine Fisheries Service and the US Fish and Wildlife Service in September 2011. Developing a quantitative understanding of factors influencing the vertical movement of swordfish will help determine the potential for targeting swordfish while avoiding sea turtles.

Despite the commercial importance of swordfish, limited tagging studies have been conducted in the North Pacific (Carey & Robison 1981, Holts et al. 1994, Takahashi et al. 2003, Sepulveda et al. 2010, Dewar et al. 2011). Carey & Robison (1981) used acoustic telemetry to follow 5 swordfish during 1 to 6 d in Baja California, Mexico. Holts et al. (1994) acoustically tracked one swordfish in the Southern California Bight for 24 h. Takahashi et al. (2003) recovered an archival tag deployed on a swordfish off the coast of Japan and examined vertical movement patterns and inferred possible tracks for the 11 mo deployment. Sepulveda et al. (2010) presented observations from 9 pop-up satellite archival tags (PSATs) that were deployed and recovered in the Southern California Bight, with deployments ranging between 1 and 89 d. Dewar et al. (2011) compiled observations from 9 and 15 swordfish tagged in the central and eastern North Pacific, respectively (8 of which, dataset CA1, are also part of this study), with fish being at liberty for 5 to 287 d. Common results across all studies are diel vertical movement patterns with occasional basking events, more frequently observed nearshore. The influence of light, temperature, and oxygen on daytime and night-time depths were also investigated (Dewar et al. 2011). Despite providing valuable insights into the vertical movement patterns and general behavior of swordfish, none of the deployments using archival and satellite tags in these studies were analyzed with recent geolocation procedures that allow for the estimation of movements between tag and release (Neilson et al. 2009, Lam et al. 2010). Calculation of the tracks allows for more detailed studies of the physical and biological characteristics along the track rather than just at the beginning and end points. This approach increases the ability to quantify the relationship between environmental factors and vertical movement patterns.

This study includes a reanalysis of prior tag data (Dewar et al. 2011) and new data spanning 8 yr (2002 to 2009), all deployed in the central and eastern North Pacific Ocean. Specific objectives were to analyze the horizontal and vertical movements of the tagged individuals to improve our understanding of swordfish behavior and help inform fisheries management practices. Recent analytical methods (Neilson et al. 2009) were used to calculate daily positions of the fish and to model the impact of environmental factors on vertical movements. This approach provides a broader and more robust assessment of swordfish depth distributions and should advance efforts to target swordfish during the daytime at depth in the longline fisheries.

MATERIALS AND METHODS

Tagging

Between 2002 and 2008, 43 Wildlife Computer PSATs, versions 2, 3, 4 and MK10, were deployed on commercial-sized swordfish caught in the Hawaii-based longline and California harpoon fisheries. Estimated weights of tagged fish ranged between 45 and 140 kg.

Central North Pacific tags

Fish in the central North Pacific were caught by Hawaii-based commercial longline fishery vessels. The tagging method was identical to that described in Polovina et al. (2008) except that tag placement differed: the hardware tethered to each tag consisted of a single strand of 1.8 mm diameter fluorocarbon line, 2 stainless steel sleeves, a single mechanical guillotine (to prevent tag implosion if the tag traveled deeper than 1500 m), and a 3.5 × 1.7 cm modified titanium dart head. The fish selected for tagging were usually caught during the first 2 h of the gear-hauling phase, to maximize the condition of tagged fish. If fish were in good condition, their branch line was released from the longline and immediately transferred to a 40 m braided tarred line. The fish was then brought to the side of the vessel and tagged using a modified harpoon with a stainless steel applicator. The tag was anchored at a depth of 10 to 12 cm mid-to-posterior to the base of the dorsal fin. The fish was subsequently released by severing the leader closer to the hook.

Eastern North Pacific tags

The tags were rigged similarly as described above, although 2 different anchor types were used: a black umbrella dart (see photo in Domeier et al. 2005) and a white nylon dart with 2 additional hinged flanges, similar to a spear fishing head (Dewar et al. 2011). The tags were deployed off Southern California by the local harpoon fleet. When a swordfish was sighted, a harpoon modified to hold the dart applicator tip was used to tag the fish at the base of the dorsal fin.

Tag programming and processing

Programmed tag durations varied from 180 to 305 d.

Temperature bins for time-at-temperature data recording were manually set to 14 bins for the MK10 tags: <0, 0–5, 5–7.5, 7.5–10, 10–12, 12–14, 14–16, 16–18, 18–20, 20–22, 22–25, 25–27.5, 27.5–30, >30°C. Similarly, the depth bins were set to <1.5, 1.5–5, 5–20, 20–50, 50–75, 75–100, 100–150, 150–200, 200–300, 300–400, 400–500, 500–750, 750–1000, and >1000 m. The PAT2, PAT3 and PAT4 tags had 2 fewer bins. To allow for comparisons, the additional bins on the MK10 tags were pooled, and distributions were computed on the same 12 bins across tags (Howell et al. 2010). The binning schemes of 2 central Pacific tags (#52498 and #64219) precluded their inclusion in the analysis of depth and temperature distributions.

The binned data, as well as the profile-depth-temperature (PDT; 8 discrete temperature and depth values collected during each time bin) data, were collected over time intervals of 2, 4, 6 or 8 h, depending on the tag. All tags were programmed to GMT time.

Light levels recorded by the tags were used to estimate positions of the fish (light-based geolocation). Light levels are not measurements of absolute values of irradiance, but rather relative values ranging from ~50 (no unit) for a covered sensor to ~180 in a bright room (PAT4 Manual, Wildlife Computers, www.wildlifecomputers.com/Downloads/Documentation/PAT4%20Manual.pdf). Light sensors are not calibrated between tags by the manufacturer.

All raw data transmitted via Argos satellites were re-processed in 2009 with the latest available version of the manufacturer software, WC-AMP (which translates the raw Argos messages into binned data), and WC-GPE (which produces preliminary geolocation estimates from the tag's light level data). This allowed us to obtain the binned and preliminary geolocation data in a consistent manner across all tags (Howell et al. 2010).

Geolocation

All tracks were processed using the 'Track&Lock' geolocation filter (Table 1) developed at Collecte Localisation Satellites (CLS), France, in the MATLAB environment (www.mathworks.com/products/matlab) (Royer et al. 2005, Royer & Lutcavage 2008, 2009, Neilson et al. 2009). The algorithm relies on a state-space model to represent process (movement) and observation uncertainty. Track&Lock uses sea surface temperature (SST) and bottom topography data to better constrain the tracks. An ensemble Kalman filter is applied to solve for the trajectory, thus estimating the state vector and its covariance from a set of samples rather than the usual deterministic equations. This allows one to account for non-linear features such as sharp and convoluted thermal gradients, and include the effect of boundaries such as coastal and bathymetric features. SST fields were provided at a 9 km resolution by a blended microwave and infrared SST product from REMSS, while bottom topography data (to estimate movement constraints) were retrieved from ETOPO2 (Smith & Sandwell 1997). For some of the fish that stayed close to the coast, the diffusion parameter of the state-space model had to be adjusted manually to lower values to ensure the fish's track did not cross Baja California into the Sea of Cortez (the bathymetry data constrains the fish to sea areas, but if the diffusion parameter is too high, plausible presence areas emerged in the Sea of Cortez).

For N = 4 tags, we were unable to obtain convergence with the above method, and the 'trackit' package, developed by A. Nielsen for the R environment (The R Project for Statistical Computing, www.r-project.org) at the School of Ocean and Earth Science and Technology, Hawaii, USA, was used as an alternative (Nielsen & Sibert 2007, Lam et al. 2008, 2010, www.soest.hawaii.edu/tag-data/trackit/).

Both tools rely on light data, a state-space model to estimate the position of the fish, and an extension of the Kalman filter to solve the optimization problem. Trackit possesses the capability to use sea surface temperature as well, but our attempts to include that information were unsuccessful, so only light information was used for those 4 tracks, and the resulting tracks were then linearly interpolated to obtain 1 position per day, matching the output of both methods.

Table 1. *Xiphias gladius.* Summary of deployments of pop-up archival tags on swordfish in the central and eastern North Pacific from 2002 to 2009. Some weights were not documented during tagging. For some tags geolocation was not possible. Dates: mm/dd/yy. Lat.: latitude, lon.: longitude

Argos ID	Serial ID	Tag type	Weight (kg)	Deployment Date	Lat. (°N)	Lon. (°E)	Pop-up Date	Lat. (°N)	Lon. (°E)	Days of data	Geolocation
8832[b]	02P345	PAT2	73	10/31/04	33.23	241.97	11/24/04	32.9	242.48	24	No
19203	02P0439	PAT2	68	09/11/02	33.2	241.9	10/23/02	22.3	228	42	No
19910	02P0469	PAT2	45	11/16/02	35.48	229.7	01/20/03	7.19	216.18	64	No
30319	02P0639	PAT2	45	02/09/03	30.88	205.65	02/28/03	24.66	205.37	18	trackit
30406	02P0604	PAT3	79	12/16/03	32.69	242.19	02/14/04	25.73	218.63	59	No
30410	02P0605	PAT3	113	11/04/03	33.2	241.95	12/15/03	32.11	241.87	40	trackit
40560	02P0603	PAT3		11/20/03	33.21	241.9	12/24/03	20.9	236.32	34	Track&Lock
41732	03P0173	PAT3	68	10/30/04	33.32	241.87	02/15/05	17.92	247.53	105	Track&Lock
41737	03P189	PAT3	82	10/23/04	33.27	242.05	04/11/05	25.57	217.84	170	Track&Lock
49070[a]	03P0599	PAT4	90	03/26/05	24.27	213.45	04/07/05	21.69	212.21	10	Track&Lock
52498	04P0175	PAT4	60	03/28/05	24.45	213.92	08/26/05	41.76	207.63	147	trackit
59270	05P0010	PAT4	73	11/05/05	33.48	241.88	01/18/06	5.26	239.96	71	Track&Lock
59275	05P0026	PAT4	91	09/04/05	33.88	241.79	12/16/05	17.5	237.73	101	Track&Lock
59276	05P0029	PAT4	91	09/04/05	33.33	242.25	02/22/06	22.47	249	167	Track&Lock
64219	06A0109	MK10	120	07/03/06	27.82	212.04	12/14/06	39.62	228.09	163	Track&Lock
67457	06A0220	MK10	91	11/24/07	33.37	241.91	05/22/08	31.92	229.08	180	Track&Lock
67458	06A0221	MK10	91	08/30/07	33.04	242.45	02/26/08	−1.34	217.19	180	Track&Lock
67461	06A0225	MK10		08/25/08	33.02	242.15	10/06/08	32.9	241.89	39	trackit
67462	06A0227	MK10	118	11/19/07	33.35	241.88	01/06/08	31.44	241.32	47	Track&Lock
67463	06A0228	MK10		07/23/08	33.15	242.4	11/27/08	32.72	242.78	125	Track&Lock
67464[b]	06A0230	MK10	91	11/15/08	33.39	241.79	12/04/08	32.93	242.52	19	No
67465	06A0231	MK10		08/25/08	33.04	242.16	02/22/09	30.86	241.9	179	Track&Lock
67466[a]	06A0232	MK10	91	11/20/07	33.52	241.82	02/02/08	31.29	206.68	98	Track&Lock
75939[a]	07A0171	MK10		10/29/08	33.25	242.35	11/28/08	32.73	242.79	28	Track&Lock
88148	08A0602	MK10		12/06/08	32.73	242.52	06/04/09	18.97	220.03	171	Track&Lock
88149	08A0603	MK10		10/20/08	33.21	242.39	01/13/09	26.88	245.67	82	Track&Lock
88150	08A0604	MK10		10/16/08	33.32	241.97	02/08/09	33.89	226.46	112	Track&Lock
88151	08A0605	MK10		10/17/08	33.32	242.28	04/15/09	27.08	225.66	178	Track&Lock

[a]Recovered tag; [b]recovered tag that did not transmit

Environmental variables

Environmental variables that were extracted along the tracks include the following: dissolved oxygen (World Ocean Atlas; WOA), chlorophyll *a* (chl *a*) concentration (MODIS-Aqua), photosynthetically active radiation (PAR; MODIS-Aqua), SST (AVHRR Pathfinder v4 and GAC), mixed layer depth (MLD; Naval Research Laboratory), thermocline depth, moon illumination, and time of sunset and sunrise (US Naval Observatory). The WOA (Boyer et al. 2006) provides objectively analyzed climatological fields of *in situ* data at standard depth levels for annual, seasonal, and monthly compositing periods for the world's oceans and is available online at www.nodc.noaa. gov/OC5/WOA05/woa05data.html. We used monthly 1° data for all analyses. We used 4 km weekly data for MODIS, available from NASA's Goddard Space Flight Center website (http://oceancolor.gsfc.nasa. gov). The 9 km weekly Pathfinder data is available on the National Oceanographic Data Center website (www.nodc.noaa.gov). The 1° monthly climatologies of MLD were constructed by the Naval Research Laboratory (www7320.nrlssc.navy.mil/nmld/nmld .html). Astronomical data from the US Naval Observatory are available at www.usno.navy.mil/USNO/ astronomical-applications. Thermocline depth was computed from the PDT data and from the WOA following the method described in Polovina et al. (1995) as the depth at which the temperature gradient is maximal. When the fish was staying at depth or at the surface, the thermocline depth information was just considered as missing for that particular time period.

Separation of day and night

To characterize daytime behavior, great care was taken to separate daytime from night-time and to exclude crepuscular periods (transition behavior). To achieve this, the US Naval Observatory's sunrise and sunset data were used to identify the latest time of sunrise and earliest time of sunset in GMT time along each track, to define a 'pure daytime' period common to every day of the track.

Time-bin programming varied from tag to tag (2, 4, 6, 8 h), and some time bins overlapped sunrise or sunset and had to be discarded: for some tags, the remaining daytime period used in the analyses was much shorter than the actual duration of daytime. As a result of this approach, it was not possible to identify a daytime period of equal duration for all tags (10:00 to 14:00 h local time for example). Durations of the estimated 'pure daytime' periods varied between tags, but the priority was to use as many tags as possible in the analysis. The term 'daytime' hereinafter refers to the estimated 'pure daytime.'

The same approach was used to obtain 'pure night-time' periods.

Mean depth

Mean daily depths were estimated from the time-at-depth (TaD) data for each daytime and night-time period and calculated as the sum of the product of the bin frequency multiplied by the bin interval mid-point. Daytime mean depth was used as a proxy for daytime foraging depth. As this approach can introduce biases in the mean depth values obtained, depending on the width of the programmed depth bins, daytime mean depth was also computed directly from the archived data for the recovered tags and compared to daytime mean depth computed from the TaD data those tags transmitted so that potential biases could be estimated.

Generalized additive models

We used generalized additive models (GAMs; Hastie & Tibshirani 1990) to model the relationships between daytime mean depth and various environmental parameters: depth of various oxyclines (0.5, 1, 2 ml l^{-1}) and isotherms (5, 8, 20°C), depth of the thermocline (from the PDT data and WOA), mixed layer depth, as well as oxygen concentration and temperature (interpolated from the PDT data) at various depths, chl a concentration and PAR.

As the variable of interest was daytime foraging at depth, we removed all basking events (daytime bins for which the time spent in the 2 shallowest depth bins was not zero, or all daytime depths < 50 m for the archival data) from the time series before computing the GAMs.

GAMs were constructed in R (v2.11.1) using the 'gam' function of the 'mgcv' package (Wood 2006). The Gaussian family with an identity-link function was used. Model selection was performed manually, and we retained candidate predictors that were statistically significant at the 0.05 level, minimized the general cross validation (GCV; Wood 2006) score, and improved the predictions. All candidate variables were modeled as continuous variables. We set gamma = 1.4 to avoid overfitting (Wood 2006), and penalized regression smoothers were used. Basis dimensions for these were chosen according to the 'choose.k' method described at http://stat.ethz.ch/R-manual/R-devel/library/mgcv/html/choose.k.html but subsequently manually adjusted to 'straighten' the smoothers and further avoid overfitting.

Potential confounding between statistically significant covariates was investigated with variance inflation factors (Graham 2003, Kutner et al. 2005) using the 'vif' funtion of the 'HH' package.

Model predictions were made via the 'predict' function of the 'mgcv' package. We computed predicted daytime mean depth for individual tracks, as well as monthly prediction maps. To make the prediction maps more legible, the kriging function 'krige.conv' from the R package 'geoR' was used. For individual track predictions, the model was computed for all tags except the tag of interest, and the predictions were then run for the tag data (leave-one-out method).

RESULTS

Tagging

Of the 43 tags deployed, only 28 tags yielded usable data (Table 1, Figs. 1 & 2); 9 never reported; 3 popped off ('popped-up') and reported, but transmitted no data; and 2 transmitted data, but based on the depth data the animals apparently died right after deployment (Domeier et al. 2003). One earlier tag (PAT2) transmitted data, but the reprocessing with a newer version of the software yielded no usable data.

Tag deployments ranged from 10 to 180 d. The entire archived record was obtained from 5 recovered tags (see Table 1).
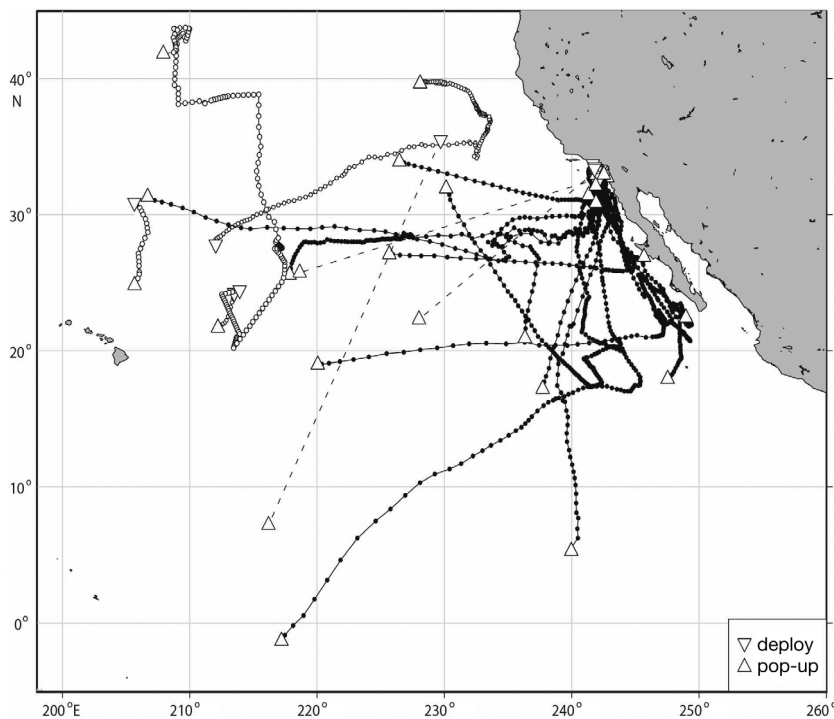
Fig. 1. *Xiphias gladius*. Tag deployments (n = 28) for the period 2002–2008. Dots: daily positions along tracks. Dashed lines: tags for which tracks could not be obtained. White and black dots: fish tagged in the central and eastern North Pacific, respectively

Horizontal movements

Of the 28 tags from which data were obtained, tracks were estimated for 23 tags (Figs. 1 & 2, Table 1).

For the 2 recovered tags that did not transmit data, it was not possible to estimate geolocations using the raw light data and no tracks were obtained. Geolocation was not possible for 3 of the earlier tags (PAT2/3, Table 1) either, possibly because of poor light records.

The northernmost and southernmost positions reached by a fish during our deployment period were 43.7°N (tag #52498) and 1.3°S (tag #67458), respectively.

We compiled the percentages of days without preliminary geolocation estimates (obtained with the manufacturer's software from the light data) or SST information for each tag. These gaps amounted on average to 58 and 25% respectively, and 15% for days with neither information. Fig. 3 shows the time series of state-space model estimated and tag-derived longitude, latitude and SST for all the tracks processed with the Track&Lock method. Average errors ranged from 0.5–25.6°, 4.1–28.9°, and 0.3–

3.9°C for longitude, latitude and SST, respectively. Median errors ranged from 0.2–21.6°, 1.2–13.2°, and 0.2–3.6°C, respectively.

Of the 24 fish tagged off San Diego (for the tags for which a track could not be obtained, the analysis is based on movements between deployment and pop-up locations), 15 radiated away from California, following a primarily south-southeast course before diverging into the central North Pacific or along the coast of Baja California, while 9 remained in the vicinity of San Diego, 1 of them for the full 180 d of the track (Figs. 1 & 2). One of the central Pacific tags (#64219) followed a north-eastward course approaching the California coast (~234°E) before turning towards the north-west. The remaining 3 first followed a southward course. The longer track (tag #52498) then switched to a northward course in May (Fig. 2).

Mean and median daily speeds across all tracks were calculated at 22.7 and 13.1 km d^{-1}, respectively. When daily speeds were computed as 5-d moving averages to obtain more robust estimates, mean and median daily speeds were calculated at 22.6 and 13.1 km d^{-1}, respectively.

Vertical movements

Swordfish encountered a broad range of depth and temperature. Temperature and depth ranges for all fish combined were 3.2 to 28.8°C and 0 to 1227 m, respectively; 5 fish dove as deep as 1200 m.

Mean SST from MODIS estimated along the tracks across tags was 19.9°C (ranging between 13.4 and 27.9°C). The minimum temperature measured by the tags during the daytime (in absence of basking) ranged from 3.8 to 17°C with a mean of 7.0°C.

Data from 26 tags with similar binning strategies were pooled together (Fig. 4a). The depth data showed a bimodal distribution, with swordfish spending 60 and 22% of their time between 0 and 100 m and between 200 and 400 m, respectively. They only spent 7% of their time below 500 m. Similarly, the temperature distribution exhibited 2 modes, one between 7.5 and 10°C and another between 16
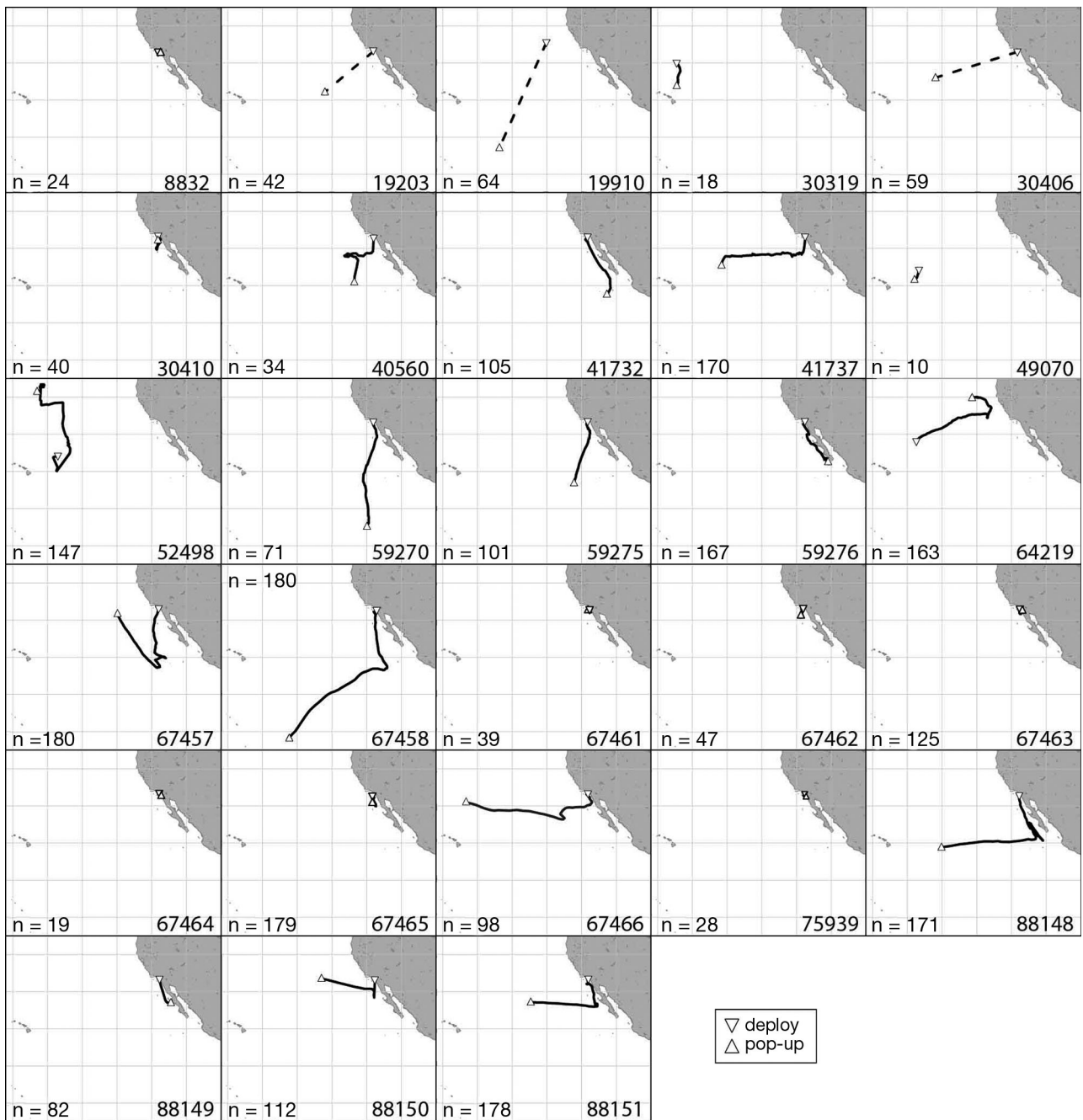
Fig. 2. *Xiphias gladius.* Individual tracks for 28 tags. Dashed lines: tags for which tracks could not be obtained (including tags #8832, #19203, #19910, #30406, and #67464). n: number of days at liberty for each tag

and 18°C, where fish spent 22 and 20% of their time, respectively.

Daytime and night-time distributions are shown in Fig. 4b,c. Because of the different bin intervals used across tags, only 20 tags had time bins that could be characterized as daytime bins and 22 as night-time bins. Classic diel movement (shallow at night, be-

tween 0 and 100 m, versus deeper than 200 m during the day) was observed, with the exception of occasional daytime basking occurring in the general area of the California current in the fall and winter (Figs. 4 & 5). During the day (Fig. 4b), 66% of the fish's time was spent at depth, between 200 and 750 m, corresponding to 65% of the time spent between 5 and

Fig. 3. *Xiphias gladius*. Time series of state-space model estimated (black line) vs. tag-derived (X) longitude, latitude and sea-surface temperature (SST) for all the tracks processed with the Track&Lock method. Green and red triangles: points of release and pop-up of each tag, respectively
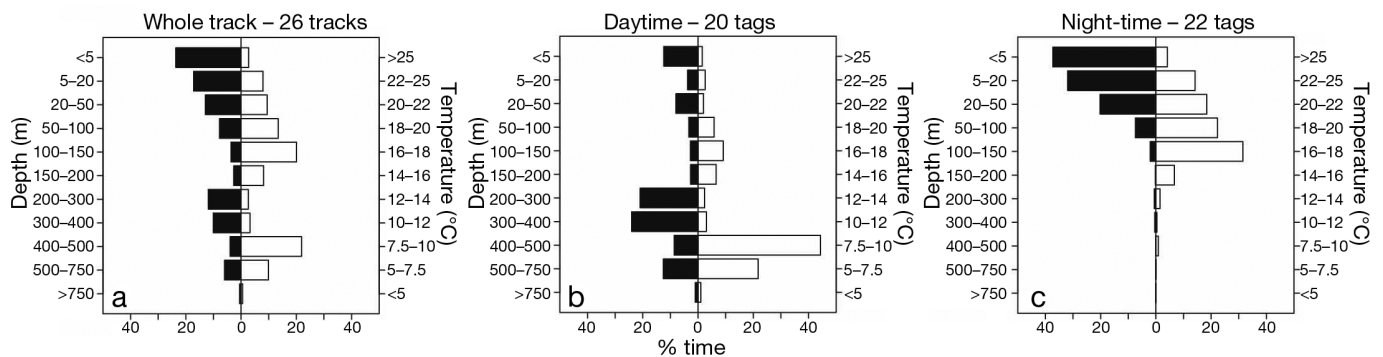

Fig. 4. *Xiphias gladius*. Distribution of percent time spent at each depth or temperature bin for all tag data pooled together (a) over whole tracks, (b) during daytime, (c) during night-time

10°C, while 24% of the time was spent above 50 m (basking). During the night (Fig. 4c), 97% of the animals' time was spent above 100 m, 37% of which was spent near the surface (<5 m), which corresponds to 91% of swordfish time >16°C, with a peak between 16 and 18°C (31%).

Archival records from the recovered tags were used to check the agreement between estimated daytime/night-time and observed dive patterns (Fig. 5). Fig. 5 shows the depth records for tags #75939 and #49070. Both records confirm that the estimated daytime and night-time periods did not include any crepuscular period.

For tag #49070 (Fig. 5 tagged close to Hawaii), the limits of the estimated daytime periods matched closely the diel movement of the fish. The fish
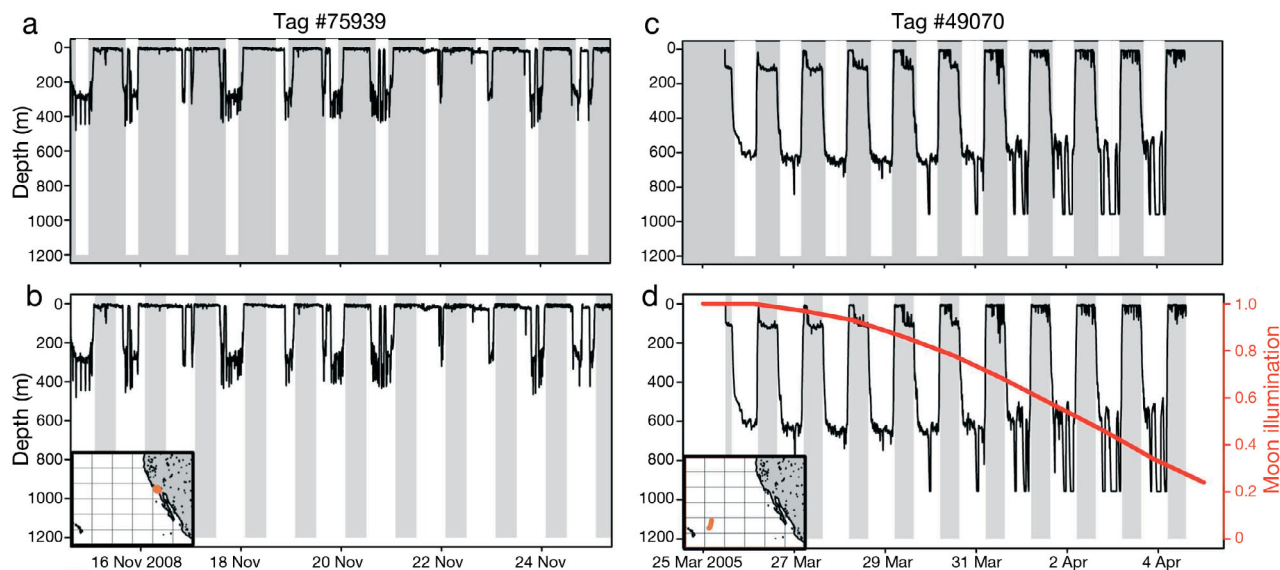
Fig. 5. *Xiphias gladius*. Depth records from 2 recovered tags; #75939 (11 d selected from the whole track for better legibility) and #49070. (a,c) White areas: estimated daytime periods, (b,d) gray areas: estimated night-time periods. Insets: respective estimated tracks. (d) Red line: moon illumination (1 = full moon, 0 = new moon)

seemed to start diving shortly before sunrise, stay at depth during the whole day, and ascend to shallow waters around sunset. During estimated night-time periods, the fish made frequent shallow dives (up to 200 m). However, for tag #75939 (Fig. 5), which stayed close to San Diego for 28 d, the pattern was not as obvious. The general bell-shaped dive pattern was the same as for tag #49070 on most days, but often featured excursions to the surface during the day (basking). On occasion, a majority of the daytime was spent at the surface. At night, the fish stayed almost exclusively at the surface.

Fig. 5d also shows moon illumination along tag #49070's track. It was full moon at the very beginning of the track and close to new moon by the end of it. This variation in illumination at night coincided with a transition of the fish from ~107 to 15 m.

Once basking events were removed from the data, the overall average daytime mean depth calculated using the histogram data across tags was 375 m in comparison to 376 m for the recovered tags only (304, 588, 276, and 387 m for tags #8832, #49070, #67464 and #67466, respectively); daytime mean depth calculated directly from the archived data was 294, 557, 281, and 337 m for tags #8832, #49070, #67464 and #67466, respectively; data for tag #75939 had to be excluded from this analysis since the fish basked almost every day along the track. The difference between the 2 methods in calculating the average daytime depth ranged from 5 to 50 m.

Oxygen limitation

Fig. 6 presents daytime dive ranges (min and max depths for each time bin, from the PDT data) overlaid onto contours of dissolved oxygen concentration along the track for tag #59276 (Fig. 6a), where the fish followed the coast of Baja California and tag #67466 (Fig. 6b), for which the fish spent ~6 wk around the coast before swimming westward and northward of Hawaii. While the depths do not appear to follow a specific oxygen concentration, their mean depth tracks the oxycline over the course of the trajectory.

We also interpolated WOA oxygen data along the tracks to estimate the oxygen concentration at the maximum daily depths. Minimum, mean, median and maximum oxygen concentrations at maximum depths were 0.16, 0.99, 1.47, and 5.73 ml l^{-1}, respectively. The minimum oxygen concentration (tag #67457) was at a depth of 504 m, in March 2008 (at 17.7°N, 242.3°E).

Light

Carey & Robison (1981) initially hypothesized that swordfish stay around a constant light level, most likely following the diel migrations of cephalopods and other epi-mesopelagic organisms that are foraging in association with the SSL (Nelson et al. 1997, Dagorn et al. 2000, Brill et al. 2005). Since then it has
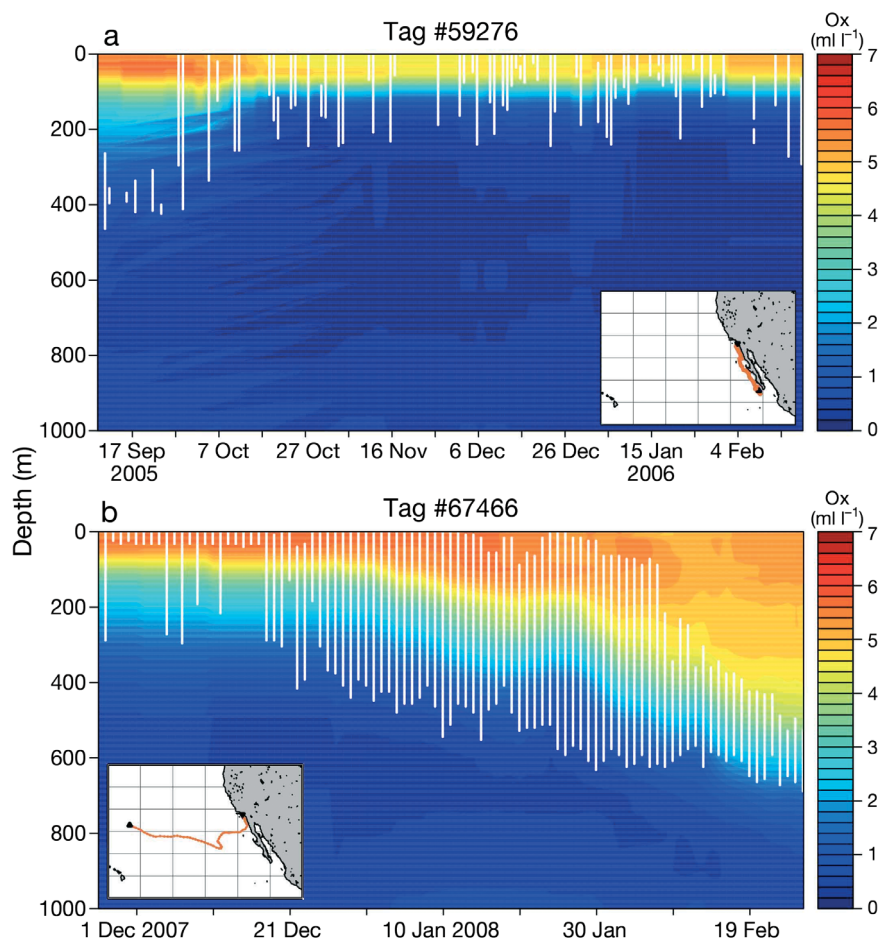
Fig. 6. *Xiphias gladius*. Swordfish daytime minimum and maximum depth (white lines) overlaid on oxygen concentration contours for tags (a) #59276 and (b) #67466. Insets: respective estimated tracks

the beginning of the track (Fig. 5d) and some very deep dives during the daytime.

Model results

After careful examination of the significance of the different environmental factors considered, 3 covariates were retained: temperature, dissolved oxygen and light. Several GAMs were designed to assess their separate and combined effects. Given that the WOA only has information for dissolved oxygen at certain depths, we used oxygen at 400 m (which was the depth level available closest to the overall mean depth of 375 m). Similarly, only temperature at 400 m was retained in the models. Chl *a* concentration and PAR were used as proxies for light (Tont 1975, Matciak 1997), but only the former appeared to be a significant factor.

The respective variance inflation factors were all <2, suggesting low collinearity (Graham 2003, Kutner et al. 2005); 1.106 for dissolved oxygen at 400 m depth, 1.275 for temperature at 400 m, and 1.321 for chl *a* concentration.

Three models looked at the separate effects of chl *a* concentration, dissolved oxygen at 400 m (ox400), and temperature of the water column at 400 m (T400). Chl *a* concentration by itself explained 55% of the variation in daytime mean depth, while ox400 and T400 explained 49 and 47% of the variation, respectively. Fig. 9 shows the estimated plots of the smoothers (s) for those 3 separate models. Daytime mean depth decreased as chl *a* increased but increased as ox400 and T400 increased.

The best model combining all 3 factors was:

$$\text{daily daytime mean depth} \sim s[\log(\text{chl } a)] + s(ox400) + s(ox400, T400) \tag{1}$$

It explained ~77% of the observed deviance (Table 2). When an oxygen–temperature interaction term was included, the temperature term alone was not significant in the full model (Eq. 1).

The summaries of the individual models, the diagnostics plots, and the smooths of the combined model

been shown that swordfish do not strictly follow isolumes, especially when basking occurs (Carey 1990, Sepulveda et al. 2010). The selected 15 d depth record for tag #67466 (Fig. 7) exhibited the typical diel behavior, with the corresponding light level staying relatively constant at a very low level (~30 readings) over a 600 m depth range. In contrast, data for the selected 15 d period for tag #75939 (Fig. 7) showed basking events almost daily with light reaching levels >200.

To examine light levels experienced by fish at daytime foraging depths, average light levels in the absence of basking were examined for the recovered tags (except #75939, see above). For the 4 tags, mean hourly light levels across days without basking were computed (Fig. 8). Except for tag #49070, the mean hourly light level stayed remarkably constant over a 24 h period. Night-time light level for tag #49070 was slightly higher than daytime light level, most likely due to the full moon at
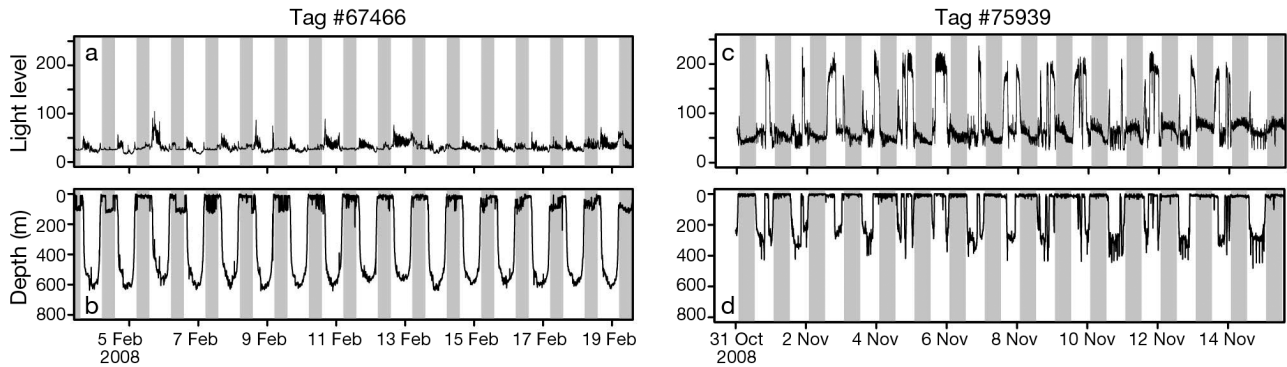
Fig. 7. *Xiphias gladius*. (a,c) Light level and (b,d) depth (m) selected records over 15 d for tags #67466 and #75939. Shaded areas: night-time periods
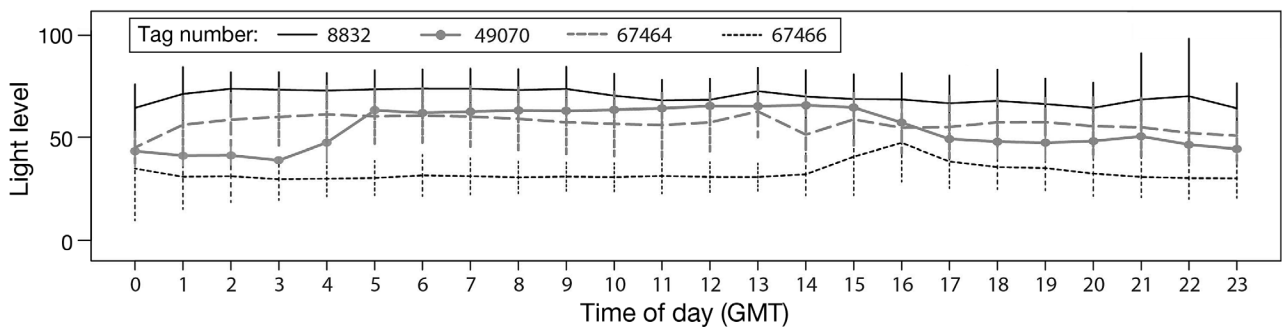

Fig. 8. *Xiphias gladius.* Typical light level (mean ± SD) over a day in the absence of basking for 4 recovered tags (tag number in box)

are available in the Supplement at www.int-res. com/articles/suppl/m452p219.pdf (Table S1, Figs. S1 & S2, respectively) to allow the reader to evaluate the validity of the model.

This model performed well in predicting daytime depth (77% of the deviance) for individual tagged fish (Fig. 10) and allowed for the development of monthly maps that predict the mean daytime depths of swordfish (Fig. 11).

A similar approach to build a model for night-time depth was attempted without success. We were unable to identify clear mechanisms or primary factors that would account for a significant portion of the variability in night-time mean depth, which showed more variability than daytime mean depth, although within a much narrower range.

DISCUSSION AND CONCLUSIONS

Our results, expanding on the analysis of Dewar et al. (2011), represent the most comprehensive tagging data set and complex analysis for swordfish in the North Pacific. Our findings emphasize the wide range of habitats swordfish occupy, from the surface to over 1200 m (Fritsches et al. 2005), with the capability of tolerating extremely low oxygen concentrations.

Tagging

Our deployments were fairly short compared to those reported by Neilson et al. (2009) in the Atlantic Ocean (up to 400 d), probably a result of different tag attachment methods and programmed deployment durations. Only 65% of the tags deployed provided usable data, and only 3 tags (7%) stayed on for the full duration of their programmed deployment period. Tag shedding is a recurrent problem with PSATs deployed on a variety of species (Gunn & Block 2001, Wilson et al. 2005, Hays et al. 2007, Holdsworth et al. 2009).

Mean depth

While the summarized data transmitted by PSAT tags masks detailed movement patterns, the mean depth obtained from the histograms provided an esti-
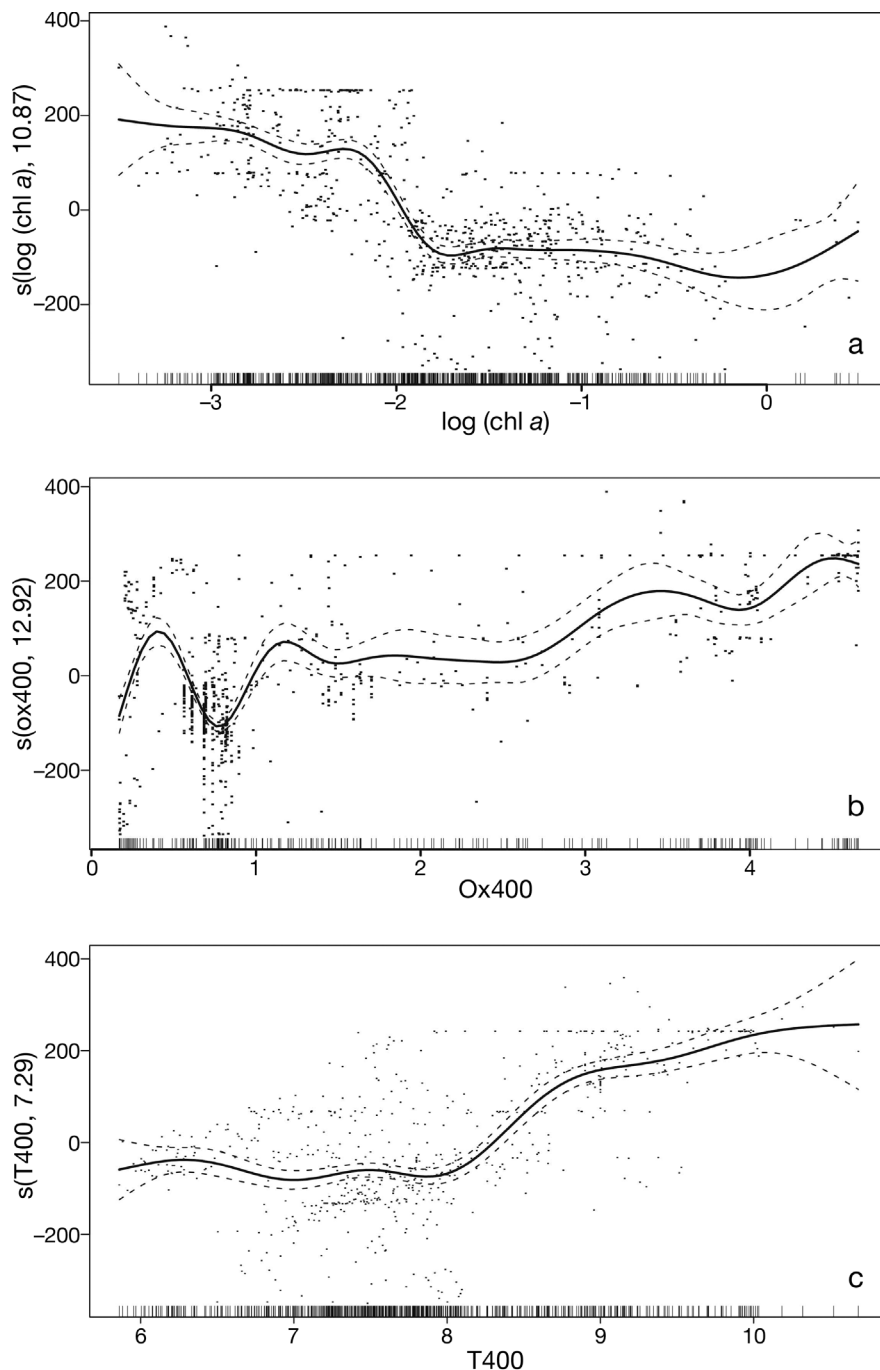
Fig. 9. *Xiphias gladius*. Estimated individual effects (solid line) on swordfish daytime mean depth of (a) chl *a* concentration, (b) dissolved oxygen concentration at 400 m (ox400), and (c) temperature at 400 m (T400). Dashed lines: 95% confidence limits, dots: residuals. Ticks at axes: values for which there is data. Positive values on *y*-axis: deeper depths

mate similar to that obtained from the archival tags providing confidence in this method. The comparison of mean depths computed from the archival and binned data differed by only 10 to 50 m.

Geolocation

Our results indicate the potential for using light-based geolocation to track swordfish over relatively long time periods.

Our geolocation errors and confidence intervals are similar to those reported by Neilson et al. (2009) for the same species and the same geolocation software and obtained using similar technology. Our study used environmental data at, or closest to, the location given by the most probable track. A better insight into the distribution of error in latitude and longitude around each daily position could allow for computing a weighted average of environmental variables, as used by Sippel (2010). This would be a more robust approach, although more precise matching of locations to environmental variables is limited by the temporal and spatial resolution of the WOA.

Geolocation proved particularly challenging for swordfish because of their crepuscular diving behavior (Holdsworth et al. 2007) and their deep and rapid dives (Carey & Robison 1981, Neilson et al. 2009), making it difficult to identify sunrise and sunset events. The use of SST and bathymetry constraints in the Kalman filter did improve the geolocation estimates (our Fig. 3; Teo et al. 2004, Neilson et al. 2009, Lam et al. 2010). Fig. 3 illustrates the weight given to the SST information in the fitting process for some of the tracks where gaps in light data were important. On the other hand, it can be noted that when light information is available and relatively clean, the fit to SST can become poor.

Fish trajectories varied greatly. Among the 24 fish tagged off San Diego, 9 stayed close to the tagging location for the whole duration of the track, while courses followed by the remaining individuals diverged into the central North Pacific or along the coast of Baja California. The 4 fish tagged in the central Pacific mostly stayed in that area. No obvious seasonal pattern seemed to

Table 2. Model summary. T400 and ox400: temperature and dissolved oxygen concentration at 400 m, respectively. edf: estimated degrees of freedom; GCV: general cross validation; scale est.: estimated scale parameter

Parametric coefficients				
	Estimate	SE	t	Pr(>|t|)
(Intercept)	380.197	2.836	134.1	$<2 \times 10^{-16}$
Approximate significance of smooth terms				
	edf	F	p	
s(log(chl a))	11.83	13.57	$<2 \times 10^{-16}$	
s(ox400)	10.52	4.59	9.7×10^{-7}	
s(ox400,T400)	17.37	14.62	$<2 \times 10^{-16}$	
R^2(adj) = 0.754	Deviance explained = 76.8%			
GCV score = 5973.1	Scale est. = 5314.7	n = 661		

explain such different patterns in horizontal movements between individual fish. Tracks obtained over longer time periods will be needed to resolve stock structure in the central and eastern Pacific.

Oxygen tolerance

Results confirm that swordfish have a high tolerance for low oxygen levels. The minimum oxygen values encountered by our fish (<0.2 ml l^{-1}) are much lower than values reported in the literature for bigeye tuna (<1.5 ml l^{-1}; Brill 1994, Musyl et al. 2003, Brill et al. 2005), and slightly lower than figures recently reported for swordfish (~0.5 ml l^{-1} minima at maximum depths; Abascal et al. 2010, Dewar et al. 2011). However, absolute values presented here are to be taken with caution given the use of 1° monthly climatologies from the WOA and the large uncertainties associated with the geolocation process (Neilson et al. 2009). Recent findings by Wegner et al. (2010) point out that 'the branching of the gill filaments in swordfish appears to increase their gill surface area above that of other billfishes and may allow them to penetrate oxygen-poor waters at depth'. Carey & Robison (1981) also suggest that swordfish's large mass of white muscle might allow them to tolerate more hypoxic conditions than tunas by accumulating an oxygen debt that they likely compensate by basking. Daytime basking was only observed in the eastern Pacific, in the general area of the California Current, where the oxygen minimum layer (OML) is much shallower than in the rest of the central North Pacific, although basking has also been observed in the

Central Pacific and Atlantic Ocean, where there is a much deeper or non-existent OML (Dewar et al. 2011).

Despite such remarkable oxygen tolerance, swordfish vertical habitat is greatly reduced in areas where the OML is shallow, as has been observed in other studies and for a range of other species (Carey & Robison 1981, Prince & Goodyear 2006, Nasby-Lucas et al. 2009, Abascal et al. 2010, Prince et al. 2010). The dive pattern for tag #59276 (Fig. 6a) shows strong evidence of hypoxia-based vertical habitat compression (Prince & Goodyear 2006, Nasby-Lucas et al. 2009, Prince et al. 2010) in the eastern Pacific, with swordfish apparently restricted to much shallower depths than in the rest of the North Pacific.

Constant isolume?

Many SSL organisms follow an isolume in their daily vertical migrations and the actual light levels have been shown to vary across species (Boden & Kampa 1967, Longhurst 1975). Based on early acoustic telemetry observations, Carey & Robison (1981) concluded that the swordfish's daily diving patterns, at least under some conditions, also tend to follow an isolume, although a later experiment with a photometer following the dusk and dawn excursions of 1 swordfish suggested that the animal was diving more rapidly than if its movement was directly controlled by light (Carey 1990).

Our results are the first empirical confirmation that, in the absence of daytime basking, swordfish stay within a very narrow range of light levels. Light level sensors are not calibrated between tags by the manufacturer, and the different light levels observed among the 4 archival tags are within the sensors' operational variability (Wildlife Computers pers. comm.). These results suggest that swordfish may be following a specific component of the SSL on which they prey during both day and night (Hays 2003, Chancollon et al. 2006).

Modeling

Using tag and environmental data along the tracks, a model was built that allows for the predic-
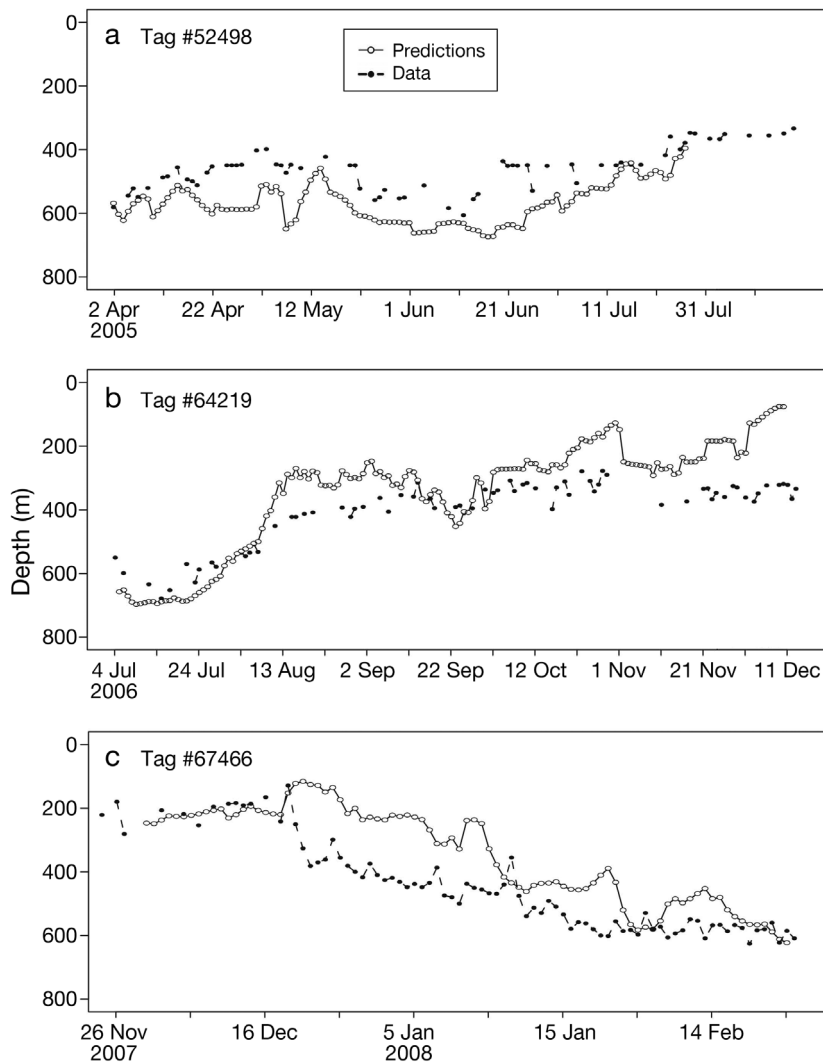
Fig. 10. *Xiphias gladius*. Model predictions and actual data for daytime mean
depth in the absence of basking for 3 individual tags

tion of swordfish daytime foraging depth. Only
environmental factors were considered (rather than
spatial or temporal, such as longitude, latitude or
month), so that the resultant model would describe
physiological or behavioral mechanisms, which, in
turn, can be translated in terms of spatial and tem-
poral variation. Only 3 factors were necessary to
describe most (77%; Table 2) of the observed vari-
ability: chl *a* concentration, as a proxy for light (in
less productive waters, light reaches deeper depths),
which affects the depth of the SSL; and dissolved
oxygen and temperature at depth, as indicators of
potential physiological constraints.

The model performed well in predicting individual
daytime mean depth over a wide variation in depth
(Fig. 10). The resulting patterns in prediction maps

produced for 2 different seasons
(Fig. 11) are in good agreement with
general patterns observed for the
depth of the SSL in the North Pacific:
from 200 m near the coast to 400 m
farther offshore in the California Cur-
rent, and ~500 to 600 m near Hawaii
(Tont 1975, Kalish et al. 1986, Johnston
et al. 2008).

Night-time mean depth was more
variable than daytime mean depth and
our attempts to use a similar modeling
approach were unsuccessful.

Potential applications of the model

The ability to predict the daytime
depth of swordfish has implications for
longline fisheries management in the
North Pacific. Hawaii-based longline
vessels targeting swordfish typically
deploy shallow sets (~60 m deep;
Bigelow et al. 2006) at night, and use
mackerel-type bait (federal regulation
to reduce turtle bycatch) and light-
sticks (Ito et al. 1998). Our results
could potentially be used to aid fisher-
men trying to target swordfish at
depth during the daytime, when habi-
tat separation between swordfish and
sea turtles is the greatest (Polovina et
al. 2003, Gilman et al. 2006, 2007,
Dewar et al. 2011). Experiments con-
ducted in Australia, with new, deep
longline settings were aimed at elimi-
nating shallow hooks to reduce by-
catch while increasing the catch of target species,
showing promise for bigeye tuna but slightly reduc-
ing swordfish catch (Beverly et al. 2004). However,
the deepest hooks were typically set ~300 m, which
would be too shallow for swordfish in most of the
North Pacific, and possibly in Australian waters. A
longline trial using Hawaii-based vessels was con-
ducted in 2002 (Boggs 2004) to test the effect of
switching to deep daytime tuna-style sets, while
maintaining the standard swordfish-style number of
branchlines per set, on the catch of marine turtles
and swordfish. Although limited to a small number of
sets (33 for control and 33 for deep setting), the trial
resulted in no catch of turtles and an 85% reduction
in swordfish catch. However, time-depth recorder
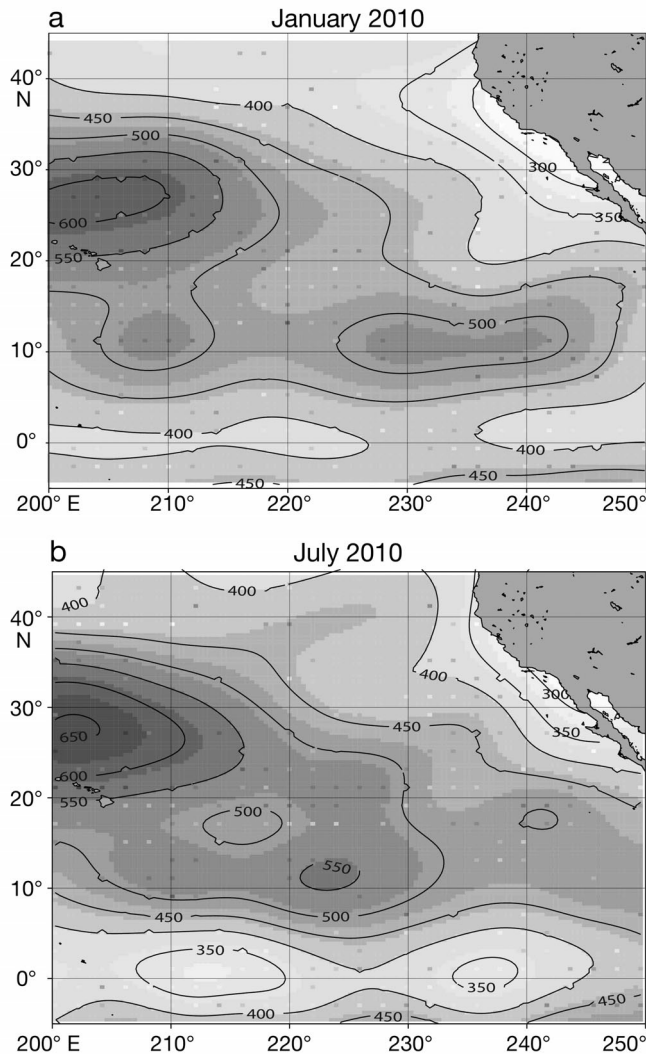data showed that the mean depth of the gear was

Fig. 11. *Xiphias gladius*. Prediction maps for North Pacific swordfish daytime mean depth for (a) January 2010 and (b) July 2010. Numbered lines: depth contours (m)

daytime depths of sea turtles in the region, although basking might complicate efforts.

Our approach, in essence, defines the vertical habitat of the part of the SSL on which swordfish prey and gives insight into how the behavior of these poorly studied organisms is influenced by their environment. The oxygen, temperature and light relationships determined by our model may reflect the physiological constraints of swordfish prey rather than swordfish themselves. Our model could be easily adapted and applied to other deep-foraging species to improve knowledge about their prey and foraging habitats and provide information about resource partitioning (Potier et al. 2007). However, as the diet of smaller swordfish differs significantly from that of larger swordfish (Young et al. 2006), our results are likely only valid for the size ranges presented here: 45 to 120 kg, or 147 to 211 cm (Uchiyama et al. 1999).

Finally, our tagging data set, in conjunction with the GAM we designed, will help parameterize a configuration of the SEAPODYM model (Lehodey et al. 2008, 2010, Senina et al. 2008, Lehodey & Senina 2009) that is being built for swordfish in the Pacific. SEAPODYM is an age-structured spatially explicit population dynamics model. Initial parameterization includes definition of temperature preferences, oxygen tolerance, foraging habitat, and speed of the animals. Once fully parameterized, such a model should be able to resolve the stock structure of swordfish in the Pacific Ocean and will allow the exploration of the impacts of different climate change scenarios on swordfish habitat. In particular, OMLs are forecast to expand (Stramma et al. 2010), which could result in further habitat compression.

244 m, typical of bigeye tuna sets (Boggs 2004); which is shallower than the daytime depth of swordfish in this region according to our results (Fig. 11). Another study conducted using Hawaii-based vessels eliminated all hooks shallower than 100 m and dramatically reduced the bycatch of incidental species, with no impact on the catch of bigeye tuna (Beverly et al. 2009).

Further field trials could be carried out in the area where Hawaii-based longline vessels targeting swordfish typically operate to examine the viability of deeper (500 to 600 m) daytime sets.

Deep day sets should be easier to deploy in the eastern North Pacific in the California Current where daytime depths of ~300 m are closer to the surface than in the central Pacific but still below the typical

between the Joint Institute for Marine and Atmospheric Research (JIMAR) and NOAA. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA or any of its subdivisions.

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