FISHERIES OCEANOGRAPHY

FISHERIES OCEANOGRAPHY *Fish. Oceanogr.* 19:4, 279–289, 2010

Fine-scale movements of the swordfish *Xiphias gladius* in the Southern California Bight

CHUGEY A. SEPULVEDA,[1,]* ASHLEY KNIGHT,[1,2] NICOLE NASBY-LUCAS[1,†] AND MICHAEL L. DOMEIER[1,†]

[1]*Pfleger Institute of Environmental Research, Oceanside, CA 92054, USA*

[2]*Institute for Applied Marine Technology, California State University, Monterey Bay, Monterey, CA 93955, USA*

ABSTRACT

This study reports on the fine-scale movements of swordfish (*Xiphias gladius*) outfitted with pop-off satellite archival transmitters (PSATs) in the Southern California Bight (SCB). PSATs were deployed on basking swordfish using traditional harpoon methods from 2004 to 2006. Transmitters were programmed for short-term deployment (2–90 days) and re-acquired using a signal direction finder. High-resolution (min^{-1}) depth and temperature data from nine swordfish (approximately 45–120 kg) were collected (>193 days). All swordfish displayed diurnal vertical movements similar to those reported for other geographic locations. The dominant diurnal movement pattern entailed swordfish remaining below the thermocline (>68 ± 15 m) during the day and near the surface, within the upper-mixed layer, at night. Collectively, the average daytime depth (±SE) was 273 ± 11 m and the average night depth 31 ± 5 m. Three distinct vertical behaviors were recorded: 35% of the records following a strict diurnal pattern, with the entire day below the thermocline and the entire night near the surface; 52% of the records revealed routine surface-basking events during the day, with an otherwise similar distribution at night; and 13% of the records exhibited surface-oriented activity during the day and night. Surface basking (<3 m during the day) was recorded for eight individuals and occurred on 131 of the 193 days (68% of the dataset). Collectively, surface basking accounted for 8% of the total daytime records. The relevance of these vertical behaviors to SCB fisheries is discussed.

Key words: fisheries, swordfish, vertical distribution, *Xiphias gladius*

INTRODUCTION

The swordfish (*Xiphias gladius*) is a pelagic, apex-predator targeted commercially throughout its extensive latitudinal range (50°N–50°S in the Pacific Ocean; Bedford and Hagerman, 1983; Hinton, 2003). This species is a global commodity, with the annual worldwide harvest estimated at over 100 000 t since 2000 (Ward *et al.*, 2000). Despite fluctuations in market dynamics, global swordfish landings have increased steadily since the 1980s, and fisheries have developed over much of the geographic range of this species (Ward *et al.*, 2000; Ward and Meyers, 2005).

In the Eastern North Pacific (ENP), swordfish are targeted with longlines, pelagic drift-gillnets (DGN) and to a lesser extent with traditional harpoon gear (Ward *et al.*, 2000; Hinton, 2003). Fleet operations typically occur near frontal zones and areas of high productivity (i.e., sea mounts, banks and islands). Over the past decade several management concerns have been raised over swordfish fisheries and their interactions with non-target species (Melvin *et al.*, 1999; Carretta *et al.*, 2003; Polovina *et al.*, 2003; Gilman *et al.*, 2006, 2007). For US fishers in the ENP, management restrictions have been implemented on longline and DGN operations in an attempt to reduce the incidental take of threatened and protected species (i.e., marine mammals, sea birds and sea turtles) (Julian and Beeson, 1998; Melvin *et al.*, 1999; Carretta *et al.*, 2003; HMS SAFE Report, 2007). Bycatch reduction strategies have directly affected US-based swordfish fishers through bycatch quotas, time and area closures, and mandated gear modifications (Hanan *et al.*, 1993; Carretta *et al.*, 2003; Uhlmann *et al.*, 2005).

Along the west coast of the USA (California, Oregon and Washington) longlining within the exclusive economic zone (EEZ) is prohibited, and the

---

**Correspondence*. e-mail: chugey@pier.org

[†]Present address: Marine Conservation Science Institute, Fallbrook, CA 92028, USA.

Received 24 March 2009
Revised version accepted 21 February 2010

doi:10.1111/j.1365-2419.2010.00543.x

principal swordfish landings (from within the EEZ) are from DGN and harpoon operations (Bedford and Hagerman, 1983; Hanan *et al.*, 1993). Although harpoon fisheries for swordfish can be effective and idyllic with respect to selectivity and limited bycatch, this method is not as efficient as longline or DGN (Ward *et al.*, 2000). The relative success of swordfish harpoon operations relies on the environmental conditions (i.e., sea-state, wind, cloud cover) as well as surface-basking rates, which may vary seasonally and inter-annually (M. McCorkle, Santa Barbara CA, USA, pers. comm.). In California, the swordfish harpoon fleet has decreased from 246 permitted vessels in 1982 to only 23 in 2006 (HMS SAFE Report, 2007). Similarly, the west coast DGN fleet has also diminished in size from over 250 vessels in 1986 to fewer than 50 active vessels in 2006 (HMS SAFE Report, 2007). The decline in participation in the west coast swordfish fisheries has occurred despite reports of a healthy swordfish ENP stock and the expansion of neighboring swordfish fisheries in Mexico (Hinton, 2003; O. Sosa-Nishizaki, Centro de Investigación Científica y de Educación Superior de Ensenada, Mexico, pers. comm.). For the DGN fishery, market dynamics, non-transferable permits and increased temporal and regional restrictions are likely the cause of the continued decline in west coast effort (Carretta *et al.*, 2003; HMS SAFE Report, 2007).

Previous swordfish movement studies

General movement trends for swordfish have been described from previous acoustic tracking studies and fisheries data, and from the use of pop-off satellite archival transmitters (PSATs) (Carey and Robison, 1981; Carey, 1990; Reeb *et al.*, 2000; Ward *et al.*, 2000; Sedberry and Loefer, 2001; Takahashi *et al.*, 2003; Markaida and Hochberg, 2005). These works have shown that swordfish typically exhibit strong diurnal movement patterns, in which daylight hours are spent predominantly below the thermocline (300–1000 m), and night hours are spent above the thermocline. These diurnal trends have been shown for swordfish in the North Atlantic (Carey and Robison, 1981; Carey, 1990; Sedberry and Loefer, 2001), West Pacific (Takahashi *et al.*, 2003) and ENP (Carey and Robison, 1981; Holts *et al.*, 1994). A deviation from this diurnal pattern includes the occurrence of periodic surface-basking events during the day. This behavior forms the basis for traditional harpoon fisheries around the world (Eastern and Western Pacific, North Atlantic, and Mediterranean) (Ward *et al.*, 2000).

Reducing bycatch and increasing gear selectivity are two major issues surrounding the future development and sustainability of swordfish fisheries along the west coast of the USA. Moving towards this goal requires knowledge of the vertical distribution of the swordfish within the SCB. The objectives of the present study were to quantify the fine-scale depth distribution and temperature preferences of swordfish in the SCB and analyze these data with respect to the two dominant commercial fisheries of the region, harpoon and DGN.

METHODS

Transmitter specifications

Wildlife Computers (Redmond, WA, USA) PAT4 and MK10 pop-off satellite archival tags (PSATs) were programmed to record depth and ambient water temperature once every minute, and light level once every 2 min. The transmitters were set for pop-off schedules ranging from 2 to 90 days, dependent on vessel availability, tag deployment location, forecasted weather conditions, and commercial fleet operations. Tag tethers were rigged with an 11-cm section of 100-kg, plastic-coated stainless-steel wire, stainless steel crimps and a black plastic umbrella anchor (Domeier *et al.*, 2005).

Tag deployment

Basking swordfish were spotted with stabilized binoculars or by spotter plane in the coastal waters (<30 nautical miles of the coast) off Southern California (approximately 33°00′ latitude, 117°30′ longitude). The PSATs were deployed using a modified harpoon adapted to insert the tag anchor a maximum of 10 cm into the dorsal musculature (Takahashi *et al.*, 2003). Size estimates, tag position and environmental conditions (i.e., water temperature and color and sea state) were documented for each tagging and tag recovery event. Field surveys of marine life present during the tagging cruises and tag recovery missions were also conducted to identify specific differences in faunal density proximal to the tagging locations.

Transmitter re-acquisition

Directed efforts to recover PSATs after their release were initiated within 24 h of receiving a signal from the Argos server. Once within 2 km of the initial pop-up location, a Gonio 400 (SERPE-IESM, Guidel, France) signal direction finder was used to triangulate the position of the floating transmitter. Upon recovery, the data were downloaded and the release pin of the tag was re-fitted by the manufacturer for subsequent deployment.

Data analyses

Archived depth and temperature data were imported into an ACCESS database (Microsoft OFFICE 2003, Seattle, WA, USA). All records were assigned 'day' or 'night' values based on the time of sunrise and sunset from the United States Naval Observatory database for Southern California. Crepuscular periods were not analyzed separately as diurnal transitions from day and night distribution patterns corresponded closely to the timing of sunset and sunrise.

Daytime depths were categorized into three distinct groups, basking, above the thermocline and below the thermocline, based on their respective depths. Basking was defined as any daytime depth record <3 m, a depth at which commercial spotter pilots can identify swordfish from the sky (D. Mauer, Carlsbad, CA, USA, pers. comm.). Individual basking events were differentiated within the track records by a change in depth in which the fish traversed the thermocline. Thermocline depth and corresponding water temperature was determined from graphical inspection of the vertical temperature profiles and identification of the strongest temperature gradient (dT/dz) for each track. 'Above the thermocline' was defined as any depth that was ≥3 m and had a lower boundary of the thermocline. 'Below the thermocline' was defined as all daytime depth records below the average depth of the thermocline.

For all tracked swordfish, basking events were examined for both duration and time of occurrence (initiation) to identify any trends specific to the behavior. For the two extended tracks which encompassed multiple months of movement data (swordfish 5 and 9) a Fast Fourier Transform was used to identify any basking periodicities (MATLAB, R12). Diurnal movement patterns for each swordfish were analyzed for differences in average depth using a two-sample *t*-test. For the calculation of average daytime depth, surface-basking periods were excluded to better reflect the actual depth occupied by any fish during the day. All values are indicated as mean ± SE. Contour plots for the joint distribution of depth and time over a 24-h period were constructed for all swordfish as well as those individuals tagged over the 2006 field season. Estimates of sea surface chlorophyll concentration were recorded for both the tagging and pop-off locations for each swordfish of this study using MODIS data obtained from Aqua and Terra EOS Satellites; processed by TERRAFIN software (http://www.terrafin.com). Light data were not used for geolocation purposes due to the limited duration of the tag deployments and the lack of adequate illumination at depth.

RESULTS

Nine swordfish tagged in the SCB from November 2004 to December 2006 provided >193 days of fine-scale (min^{-1}) depth and temperature data (Table 1). Of the nine tagged individuals, five swordfish (55%) were recaptured by commercial DGN (4) and harpoon (1) fishers. Collectively, the average swimming depth and overall depth range were significantly greater during the day (average 273 ± 11; range 235–318 m) than at night (average 31 ± 5 m; range 16–68 m) (Table 1). Similarly, all swordfish exhibited maximum dive depths during daylight hours, with the greatest depth achieved being 673 m (swordfish 3; Table 1). The greatest horizontal distance traveled by any swordfish in this study (derived from the initial tagging and pop-off locations) was 144 km (swordfish 9) and the average horizontal distance traveled for all swordfish was 30 ± 43 km.

Vertical distribution

The depth distribution data for the eight extended tracks (>24 h) revealed three distinct vertical movement behaviors during the day, while all fish remained above the thermocline at night. Behavior I consisted of swordfish remaining below the thermocline the entire day and near the surface waters at night (Fig. 1). The Behavior II vertical distribution consisted of similar average daytime depths to Behavior I; however, periodic surface basking occurred during the day (Fig. 1b). The Behavior II basking events were typically directed ascents and descents that ranged in duration from 2 to 240 min. Behavior III entailed extended periods (>240 min) of heightened surface-oriented activity (including basking), with only infrequent excursions below the thermocline (Fig. 1c).

Swordfish that exhibited the Behavior I distribution had descents and ascents that corresponded to sunrise and sunset, respectively. Behavior I was observed on 69 of the 193 days, or 36% of the entire data set. Behavior II accounted for 99 of the 193 days, or 51% of the collective data set. The number of daily surface-basking events ranged from as few as one to as many as seven (swordfish 5). Behavior III accounted for 13% of the daily records, or 25 days. This behavior was primarily observed in the two extended tracks (swordfish 5 and 9) and occurred both sporadically (1 day at a time) and in succession (on consecutive days). This behavior often entailed several hours of surface basking followed by brief (<60 min) descents and subsequent ascents to the surface waters.

To illustrate the marked similarities in the depth distribution over a 24-h period, a plot of the joint distribution of time and depth was constructed for all

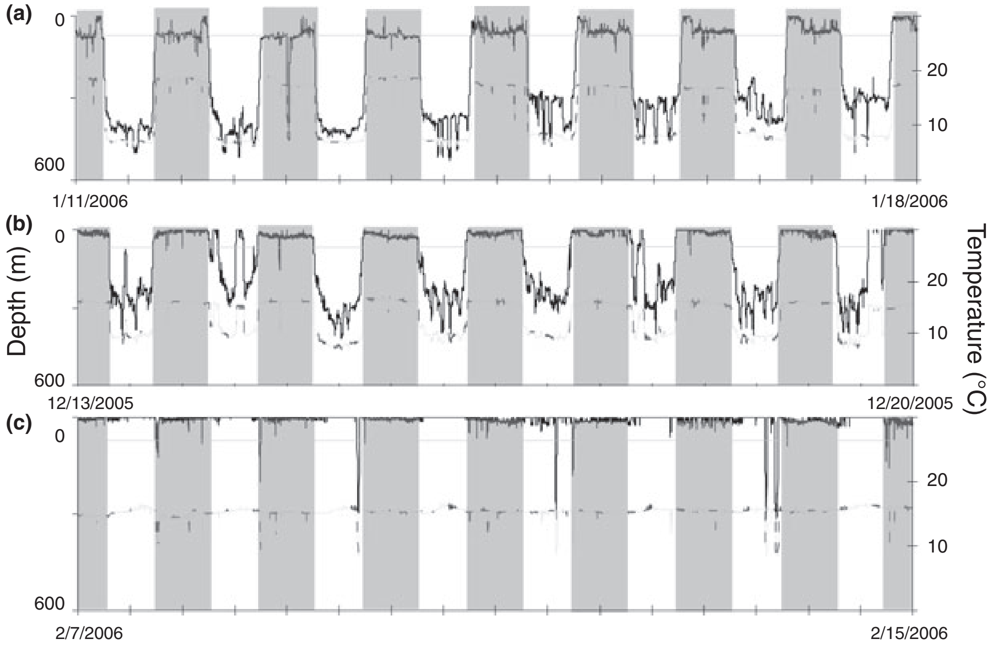
Table 1. Swordfish body size, tagging information, depth statistics and temperature information.

No.	Tag No.	Tag type	Approximately mass,* kg	Deployment	Location	Basking days	Days at liberty	Mean depth day, m	Mean depth night, m	Max. depth, m	Thermocline depth, m	ΔT,† °C
1	04P0422a	PAT4	75	11/7/2005	33°03.60′ 117°33.60′	2	4	293	16	420	57	17.6
2	04P0640	PAT4	70	12/1/2005	32°53.12′ 117°40.60′	1	1	247	69	276	66	11.1
3	04P0228	PAT4	75	7/06/06	33°05.56′ 117°52.92′	3	5	284	37	673	41	12.8
4	04P0494	PAT4	100	8/17/06	32°11.66′ 117°23.15′	0	6	318	39	436	77	11.8
5	05A0258	MK10	70	8/19/2006	33°18.00′ 118°12.00′	52	66	236	33	464	55	12.8
6	04P0422b	PAT4	80	11/5/2006	33°31.76′ 117°53.54′	5	11	287	16	492	85	15.6
7	05A0313	MK10	45	11/6/2006	33°25.23′ 117°46.34′	2	7	314	31	431	66	8.7
8	04P0485	PAT4	75	11/13/2006	33°05.60′ 117°30.98′	3	4	249	19	444	84	16.9
9	04P0635	PAT4	75	11/13/2006	32°55.83′ 117°39.61′	63	89	237	26	580	85	11.4

*Mass estimated from tagging vessel.

†Maximum difference between SST and minimum temperature at depth.

Figure 1. Three 9-day periods of swordfish vertical distribution (solid trace), corresponding water temperature during the track period (stippled red trace) and average thermocline depth (horizontal blue trace) for a 75-kg swordfish (swordfish 9). (a) Behavior 1, a distribution in which the swordfish remained at depth (approximatley 250–400 m) for all daylight hours and above the thermocline at night (shaded area). (b) Behavior II, a mixed daytime depth distribution, with periodic surface-basking events sporadically distributed throughout the depth records. (c) Behavior III, a period of heightened day and night surface-oriented activity.



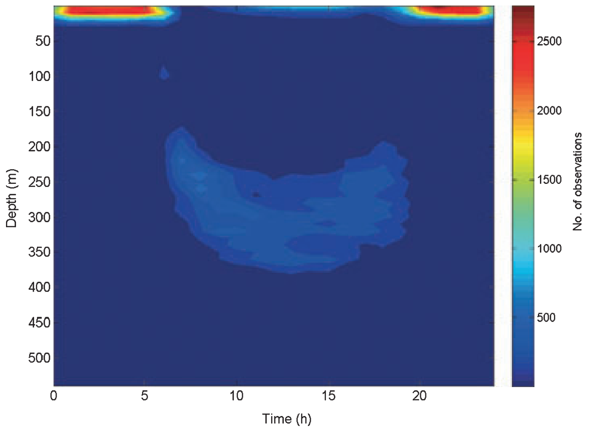


Figure 2. A contour plot showing the joint distribution of depth and time plotted over a 24-h period for all swordfish tagged in this study.

of the swordfish tagged in this study (Fig. 2). The contour plot illustrates the general depth trends over a 24-h period (approximately 0 to 30 m at night and approximately 200 to 350 m during the day). Figure 2 also shows how the depth distribution changes over the course of the day, with the maximum depths coinciding with middle of the day when illumination is typically greatest. Similarly, a binned histogram of the day and night depth distribution for all swordfish illustrates the bimodal distribution during the day (i.e., basking and below the thermocline) and the surface-oriented distribution at night (Fig. 3).

Surface basking

Surface basking during the daytime hours was recorded for eight of the nine individuals tagged, and occurred on 131 of the 193 days of data (68% of the study period). The percent of daylight hours spent basking at the surface ranged from 0 to 33% among individuals and collectively accounted for 8% of the total daytime records. For all fish exhibiting Behavior II, the average duration of the basking events was 17 ± 9 min. A daily histogram of the daytime depth distribution for swordfish 5 (66 days) shows the frequency of basking activity over the track record and the vertical distribution with reference to the thermocline (Fig. 4).

There were no identifiable periodicities in the frequency of basking events. Collectively, basking activity was found to occur at different times over the entire day and occurred over all moon phases and tidal cycles. Swordfish 9 exhibited the longest duration without any basking activity (13 days). This time period coincided with a 5-day period both preceding and following the full moon (10–20 January 2006), and was also characterized by an increased average day (158 ± 154 m versus 369 ± 56 m) and night depth (26 ± 46 m versus 73 ± 76 m). The timing of the initial ascent of all basking events was also examined over the entire day to identify further any periods of heightened basking activity (Fig. 5). Trends in basking activity were not evident, as surface basking was found to be intermittent, occurred throughout the day and often did not occur on successive days.

Temperature

Swordfish were tagged at sea surface temperatures (SST) ranging from 16.0 to 23.6°C, with an average SST (±SD) of 20.2 ± 2.4°C. Collectively, the ambient temperatures recorded during all tracks ranged from 6.1 to 23.7°C and the average SST recorded while basking at the surface was 19.1 ± 2.4°C (range; 14.4 to 23.7°C; Table 1). The average depth of the thermocline was (±SD) 68 ± 15 m and corresponded to 11.4 ± 0.3°C (Table 1). Figure 6 illustrates the range of ambient temperatures encountered by swordfish 1 over a 24-h period, showing the marked fluctuations in ambient temperature associated with the daily vertical distribution in the SCB. Figure 7 represents the diurnal temperature distribution for all swordfish of this study. Although temperatures as low as 6.1°C were

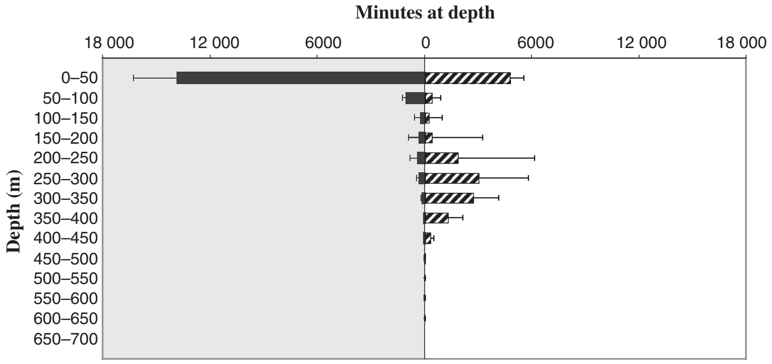
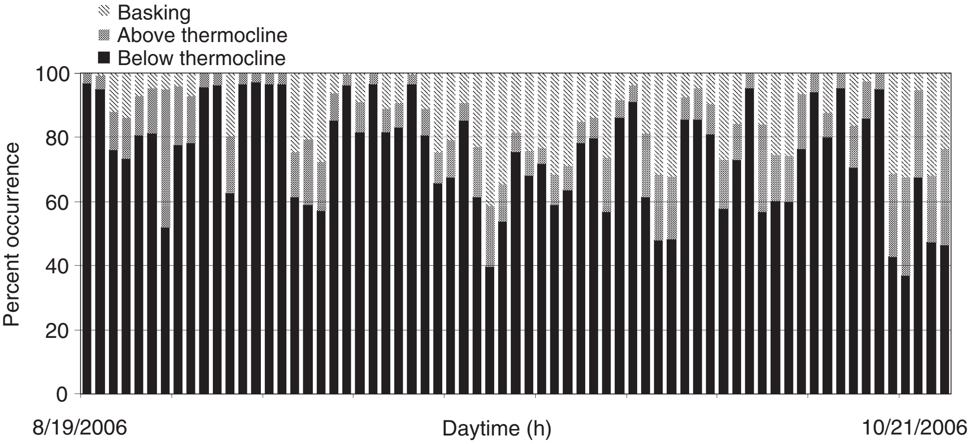


Figure 3. A binned histogram of the day and night depth distribution for all swordfish of this study (solid bars and shaded area represent night).

Figure 4. A histogram of the daytime (sunrise to sunset) depth distribution for swordfish 5 (66 days) which shows the frequency of basking activity (<3 m), time above the thermocline and time below thermocline.



recorded, the average temperature experienced at depth (below the thermocline) was 8.7 ± 0.2°C.

Additional observations

Six of the swordfish tagged in this study were found in areas with surface chlorophyll *a* concentrations ranging from 0.10 to 1.0 mg m^{-3}, while the remaining three individuals were located in areas with <0.10 mg m^{-3}. Four of the nine swordfish were tagged proximal (<1 km) to distinct bathymetric features of the SCB (i.e., banks, high spots, ridges), and five of the tags popped-off near these areas. Surveys of marine life recorded during the field tagging cruises and tag recovery missions revealed a heightened presence of marine mammals proximal to the tagging and pop-off locations (<1 km). Blue whales (*Balaenoptera musculus*), fin whales (*Balaenoptera physalus*), Rissos Dolphin (*Grampus griseus*) and Northern Elephant seals (*Mirounga angustirostris*) were concentrated near the tagging and pop-off locations.

DISCUSSION

This work reports on the fine-scale vertical movements of swordfish in the SCB and provides insight into the diurnal vertical distribution of this commercially important species. The predominant vertical distribution patterns observed in this study were consistent with those reported in previous swordfish movement studies; however, differences in average depths, basking rates and surface-oriented movements distinguish the swordfish of this study from those studied in the Atlantic and along the Baja California Peninsula (Carey and Robison, 1981; Carey, 1990).

Tagging operations

In previous studies, harpoon techniques have been used to deploy acoustic transmitters, PSATs and archival tags on swordfish in the Atlantic and Eastern and Western Pacific (Carey, 1990; Takahashi *et al.*, 2003). In the present study, the tagging procedure did not result in any immediate post-tagging mortality (based on the depth records), and appeared to result in minimal post-tagging stress, as tagged swordfish routinely returned to the surface immediately after tag implantation and dive records did not reveal specific behaviors related to the tagging event.

The relatively high recapture rate recorded in this study (55%) was likely due to the proximity of tagging activities to commercial swordfish operations (both

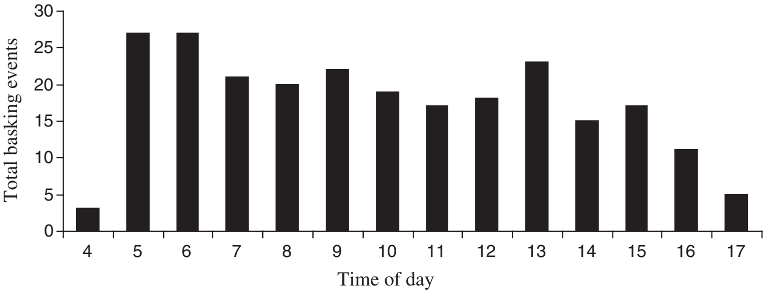
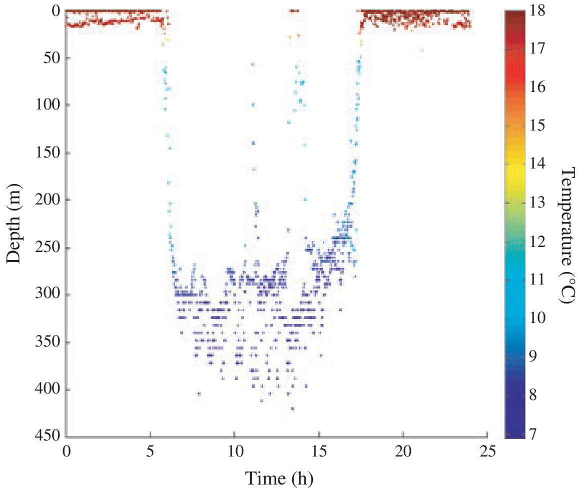


Figure 5. A binned histogram illustrating the total number of basking events (based on time of ascent) recorded over the course of the day for all swordfish in this study.

Figure 6. A binned histogram of the day and night temperature distribution for all swordfish of this study (solid bars and shaded area represent night).



DGN and harpoon). An additional factor that may have contributed to the relatively high recapture rate observed in this study is the regional closures to the DGN fishery above Point Conception which have consolidated west coast DGN effort to the SCB waters (Federal Register, 2001).

Comparisons with Atlantic swordfish

The daytime depth range found in this study was similar to that found for swordfish acoustically tracked in the Atlantic (0–600 m); however, a greater average depth was recorded in the Atlantic (approximately 500 m versus 273 m ± 11 m; Carey and Robison, 1981). The greater daytime depth may be in response to the very different oceanographic conditions of the two regions (Prince and Goodyear, 2006). In particular, differences in the thermal stratification of the water column and the presence of a strong, relatively shallow thermocline in the SCB could influence the ambient temperature at depth (Palacios *et al.*, 2004). For example, a swordfish at 300 m in the present study would experience an ambient temperature of approximately 8°C, whereas this temperature would correspond to approximately 400–600 m in the Atlantic study region (Carey, 1990). Despite the observed differences in average daytime depth, the minimum water temperatures experienced were similar [7–10°C in the Atlantic (Carey, 1990) and 8.7 ± 0.2°C (this study)] for the two regions. Although the swordfish in both regions remained at shallower depths at night (above the thermocline), the depth range in the Atlantic was much greater (0–150 m), which again may reflect the differences in thermal stratification or possibly the distribution of prey.

Additional factors that may account for some of the observed differences in vertical distribution include the availability and distribution of prey, differences in dissolved oxygen (DO) content and the overall depth of the study site. Recent work by Prince and Goodyear (2006) suggests that the differences in DO concentration at depth may act to compress the vertical distribution of pelagic fishes in the Pacific. Thus, it may be that the relatively shallow oxygen minimum layer (OML, defined as <0.5 mL L^{-1} dissolved O_2; Levin, 2003) in the ENP (approximately 400 to 600 m; Bograd *et al.*, 2008; Fuenzalida *et al.*, 2009) may account for some of the observed depth differences reported here. It must also be considered that much of the SCB study area is much shallower (approximately 400–800 m) than that of the Atlantic sites, an additional factor that could certainly limit the overall attainable depth of swordfish in this study (Carey and Robison, 1981; Carey, 1990).

Comparisons with Baja California swordfish

When compared to swordfish tracked off the tip of Baja California, the individuals of this study exhibited a greater depth range and greater average daytime depth (273 ± 10 m versus approximately 100 m) but

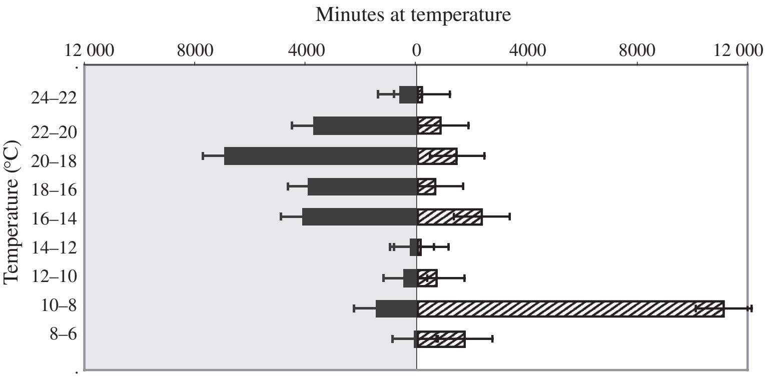


Figure 7. The joint distribution of temperature and depth plotted over a 24-h period for swordfish 1.

similar depths at night. Carey and Robison (1981) hypothesized that the relatively shallow (100 m) depth of the OML was the primary factor affecting the vertical distribution of swordfish in the Baja region. Carey and Robison (1981) also hypothesized that the shallow OML was likely responsible for the high-frequency of surface basking in the Baja swordfish, as it was suggested that the fish were surfacing frequently to recover from the hypoxic conditions experienced at depth (Carey and Robison, 1981). Because the depth of the OML may both limit the movements of the swordfish and also act to consolidate the available prey, it is difficult to tease apart the causes for the observed distribution.

In the SCB the depth of the OML is also relatively shallow (approximately 400–600 m; Childress and Seibel, 1998; Fuenzalida *et al.*, 2009), but it is approximately four times greater than that off the tip of Baja California (Carey and Robison, 1981; Prince and Goodyear, 2006; Bograd *et al.*, 2008). Hence, it may be that the upper reaches of the OML act to compress the suitable habitat of the swordfish, thus influencing the daytime vertical distribution within the Bight (Bograd *et al.*, 2008). With recent evidence supporting the shoaling of the hypoxic boundary in the California Current system, it may be that the vertical distribution of swordfish in the Eastern Pacific is a dynamic function of this hypoxic interface (Prince and Goodyear, 2006; Bograd *et al.*, 2008).

Comparisons with Western Pacific swordfish

Collectively, the suite of vertical behaviors exhibited by the swordfish in this study most closely resembles those recorded for a single swordfish outfitted with an archival tag in the Western North Pacific (Takahashi *et al.*, 2003). In the Takahashi *et al.* (2003) study, a 120-kg swordfish displayed diurnal movements resembling all three of the behavior patterns reported here (Fig. 1,b and c). Most notable was the presence of extended periods of surface-oriented behavior (similar to Behavior III in this study), which Takahashi *et al.* (2003) attributed to the transition between relatively warm and cold surface temperatures. Because the SST which preceded and followed the daytime surface activity of this study did not vary, we propose that other factors likely cued this behavior, such as the diurnal distribution of prey or possibly an increased reliance on nocturnal feeding.

The absence of vertical movements and remaining exclusively within the warm surface waters may also provide the ideal conditions for increasing the horizontal distance traveled. This has been suggested for other pelagic species (e.g. white shark, *Carcharodon carcharias*) and may be a movement pattern used when transiting through a given area (Weng *et al.*, 2007; Domeier and Nasby-Lucas, 2008). However, because of the short duration of the tag deployments and lack of horizontal movement data it is not possible to conclude whether these periods of reduced vertical activity were associated with increased horizontal displacement.

One difference between the present study and that of Takahashi *et al.* (2003) was the increased daily depth (>500 m) of the swordfish when in the 'Kuroshio Warm Water' area. During this period both the SST (>25°C) and temperature at depth (approximately 17°C at 300 m) were much warmer than that of the SCB (approximately 8°C at 300 m). It is also noted that DO concentrations at depth are different, with the OML much shallower in the ENP compared to the Western North Pacific (approximately 400–600 m versus approximately 1000–1200 m; Bograd *et al.*, 2008; Karstensen *et al.*, 2008). Additional differences from the Takahashi *et al.* (2003) work include the routine diving to ambient temperatures much lower than those reported here (<5°C; Takahashi *et al.*, 2003), suggesting that reduced water temperature was not a controlling factor for the lower depth distribution of the swordfish in this study.

Illumination, lunar and tidal cycles

In the Atlantic it has been suggested that the daily vertical movements follow a U-shaped pattern in response to the isolume (Carey and Robison, 1981). In the present study we observed a similar U-shaped daytime depth distribution in approximately 30% of the daily records (59 of 193 days). This pattern is especially evident in Fig. 2, which illustrates how the combined swordfish depth distribution changes over the course of the day. The high frequency of cloud cover in Southern California may be one reason why this was not a uniform trend among all swordfish of this study. Furthermore, Carey (1990) later reported that this depth distribution trend was not consistently observed among the swordfish tracked in the Atlantic. Similarly, the heightened surface-basking activity observed in the two extended tracks (swordfish 5 and 9) also fails to support the uniform use of the isolume for the vertical movements.

Trends in the average depth distribution over the lunar cycles were not consistent among the swordfish of this study, most likely because only segments of each period were available for analysis due to the short duration of the deployments. Of the two swordfish that contained multiple lunar cycles (swordfish 5 and 9), only fish 9 exhibited a consistently greater average night and daytime depth during the period 5 days before and after the full moon. Although data were available for two additional full-moon periods, this greater average depth was only observed during one full-moon period (15 January 2006). Although lunar-associated increases in night depth have been described for other deep diving pelagic species such as bigeye tuna (*Thunnus obesus*) and organisms of the deep scattering layer (DSL), uniform trends were not observed for the swordfish of this study (Carey and Robison, 1981; Holland *et al.*, 1992; Kringel *et al.*, 2003; Musyl *et al.*, 2003). Longer term deployments that overlap in time and space are needed to better understand periodicities in the vertical distribution of swordfish in the SCB.

Mammals

The extensive co-occurrence of marine mammals at the swordfish tagging and pop-off locations can most likely be explained by the patchy distribution of prey resources of the SCB and its increased availability along frontal edges (Hinton, 2003). In particular, the northern elephant seal was found, on repeated occasions, proximal to the tagging and pop-off locations. There is substantial overlap in the diet of swordfish and northern elephant seals, as both of these open-ocean predators have the capacity to remain at depth for extended periods and prey upon the abundant cephalopod and teleost resources associated with the SCB DSL (Sinclair, 1994; Markaida and Hochberg, 2005). These observations were corroborated by SCB swordfish fishers and spotting pilots, who agreed that SCB swordfish are frequently observed proximal to areas with high marine mammal concentrations (D. Mauer, Carlsbad, CA, USA, pers. comm.; K. Fukashima, San Diego, CA, USA, pers. comm.). The proximity of fishing operations along the productive frontal edges of the California current system is likely a factor contributing to the various bycatch issues surrounding the swordfish fisheries of the ENP (Carretta *et al.*, 2003).

How these data relate to SCB fisheries

One objective of this work was to examine the fine-scale movements of the swordfish in relation to the dominant swordfish fisheries of the region (harpoon and DGN). The depth distribution during the day was used to assess the proportion of the day that the swordfish of this study would be vulnerable to the harpoon gear type (harpoon operations occur only during the day) and the depth at night was used to estimate DGN efficacy based on current depth mandates and gear configuration (DGN operations occur only at night) (Bedford and Hagerman, 1983).

Harpoon

Basking events were evident in eight of the nine track records and accounted for only 8% of the total daytime observations. There were no identifiable periodicities in the frequency of basking events. Several inconsistencies likely account for this, which include the occurrence of basking events at different times on successive days, multiple events per day, as well as periods with no basking activity at all. The longest duration without any basking activity was 13 days (swordfish 9). The 13-day period encompassed the period before and after the full moon and occurred despite similar night and day SSTs throughout the record.

The short duration of the deployments, lack of overlapping data sets (individuals tagged at the same time) and sporadic nature of the basking activity precluded any conclusions based on individual comparisons. For the two deployments that temporally overlapped and contained basking activity, a similar basking trend was observed with both fish surfacing at approximately the same time on the same day. However, this pattern was not observed on the subsequent day, when only one fish basked and the other remained at depth (Fig. 8). Additional long-term data sets from individuals tagged at the same time and place are necessary to comprehend fully the specific factors that cue surface basking in this species.

From the data gathered to date, we propose that basking activity is cued from biotic factors that are difficult to predict, ones that probably do not remain constant over time, such as frequency of feeding, stomach fullness or body temperature. Further, we hypothesize that basking may be in response to reductions in core body temperature brought about from successful feeding at depth. Using the average temperatures recorded in this study for swordfish at depth and the surface, the average change in temperature associated with basking is >11°C. Assuming a conservative thermal rate coefficient (Q_{10}) of 2.0 (Brett and Groves, 1979; Stevens and McLeese, 1984), basking could more than double the digestion rate at depth.

DGN

The California DGN is the primary fishery for swordfish in the SCB, providing the majority of west coast swordfish landings from within the California EEZ (HMS SAFE Report, 2007). The current gear restrictions mandate a subsurface net minimum of

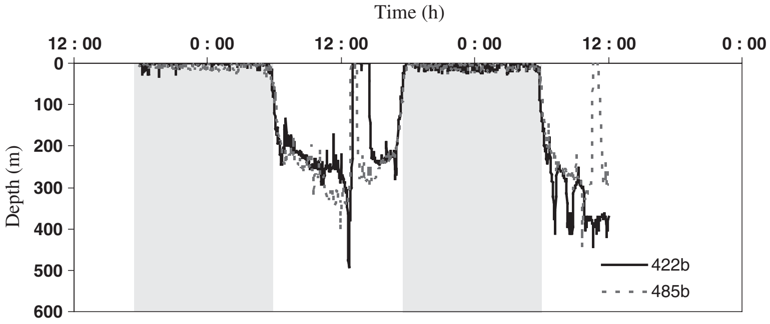


Figure 8. An overlay of the vertical distribution of swordfish 6 (solid trace) and 7 (dashed trace) for the same time period; shaded sections represent night.

approximately 11 m (36 ft suspender length), a depth selected to reduce gear interactions with marine mammals (Federal Register, 1997; Pacific Offshore Take Reduction Plan, 2008). Further increasing the minimum net depth has been recently proposed as a means to reduce additional bycatch in the DGN fishery (Sepulveda *et al.*, 2004); however, the effectiveness of these modifications relies on two main assumptions: (i) that swordfish exhibit a greater depth distribution at night compared to other non-targets taken in the fishery and (ii) that swordfish catch rates remain economically viable despite changes to the minimum gear depth. Collectively, the depth records at night showed that 54% of the time, swordfish remained within the upper 11 m (0–10.9 m) of the water column. These data suggest that the existing depth restrictions already negatively impact DGN operations considerably. Calculations based on adjusting the minimum net depth to 15 m reduce the estimated harvest by an additional 11% (65% of the distribution is <14.9 m). Given that current fishery mandates already adversely affect DGN landings (HMS SAFE Report, 2007); it is unlikely that the minimum net depth can be further altered without significantly affecting DGN efficacy and economic viability.

CONCLUSIONS

The goals of this work were to document the fine-scale movements of swordfish using PSAT technology and to correlate these movements with the fisheries of the region. Our findings suggest that although swordfish movements have been described for other geographic locations, the diurnal vertical distribution is region-specific and likely influenced by both abiotic (i.e., temperature, thermocline depth, DO content) and biotic factors (i.e., prey abundance and distribution, body temperature). Developing a greater understanding of swordfish vertical niche partitioning is key to increasing gear selectivity and reducing bycatch, two critical issues facing the future of west coast swordfish fisheries.

ACKNOWLEDGEMENTS

This study would not have been possible without the dedication and support from Thomas Pfleger, the Pfleger Family and the George T. Pfleger Foundation. Additional support was provided by Darryl Lewis and the William H. and Mattie Wattis Harris Foundation. Special thanks are offered to Captain Scootch Aalbers, Captain T.J. ‘Cowboy’ Fullam, Victoria Wintrode, Lorraine Bohnet, Leonel Romero, Diego Bernal and Jeanine Donley. Commercial fishers helped a great deal with the return of tags and tagging of individuals; we are thankful to Darren Mauer, Kelly Fukoshima (F/V *Three Boys*), Bill Sutton (F/V *Aurelia*), Tim Mulcahe (F/V *Calogera*); John Mansur (F/V *Drs Orders*) and Lance Reinhardt (F/V *Leslie Anne*). We would also like to acknowledge the support of several individuals that assisted greatly with the field studies: Corey Chan, Dan Fuller, Nicholas Sepulveda, Jack Sepulveda, Eddie Kisfaludy, Nick Wegner, Craig Heberer, Jake Ness, Trevor Young, and Jock and Charlie Albright.

REFERENCES

Bedford, D.W. and Hagerman, F.B. (1983) Billfish fishery resource of the California current. *CalCOFI Rep.* **24:**70–78.

Bograd, S.J., Castro, C.G., Di Lorenzo, E. *et al.* (2008) Oxygen declines and the shoaling of the hypoxic boundary in the California Current. *Geophys. Res. Lett.* **35:**L12607. doi:10.1029/2008GL034185.

Brett, J.R. and Groves, T.D.D. (1979) Physiological energetics. In: *Fish Physiology, Vol VIII*. W.S. Hoar, D.J. Randall & J.R. Brett (eds) New York: Academic Press, pp. 279–352.

Carey, F.G. (1990) Further observations on the biology of the swordfish. In: *Planning the Future of Billfishes*. R.H. Stroud (ed) Savannah, GA: National Coalition Marine Conservation, pp. 103–122.

Carey, F.G. and Robison, B.H. (1981) Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fish. Bull.* **79:**277–292.

Carretta, J.V., Price, T., Petersen, D. and Read, R. (2003) Estimates of marine mammal, sea turtle, and seabird mortality in the California Drift Gillnet Fishery for Swordfish and Thresher Shark, 1996–2002. *Mar. Fish. Rev.* **66:**21–30.

Childress, J.J. and Seibel, B.A. (1998) Life at stable low oxygen levels: adaptations of animals to oceanic oxygen minimum layers. *J. Exp. Biol.* **201:**1223–1232.

Domeier, M.L. and Nasby-Lucas, N. (2008) Migration patterns of white sharks *Carcharodon carcharias* tagged at Guadalupe Island, Mexico, and identification of an eastern Pacific shared offshore foraging area. *Mar. Ecol. Prog. Ser.* **370:**221–237.

Domeier, M.L., Kiefer, D., Nasby-Lucas, N., Wagschal, A. and O'Brien, F. (2005) Tracking Pacific bluefin tuna (*Thunnus thynnus orientalis*) in the northeastern Pacific with an automated algorithm that estimates latitude by matching sea-surface-temperature data from satellites with temperature data from tags on fish. *Fish. Bull.* **103:**292–306.

Federal Register (1997) Taking of marine mammals incidental to commercial fishing operations; Pacific Offshore Cetacean Take Reduction Plan Regulations. *Fed. Regist.* **62:**192.

Federal Register (2001) Endangered and threatened wildlife; sea turtle conservation requirements; taking of threatened or endangered species incidental commercial fishing operations. *Fed. Regist.* **166:**165. microfiche.

Fuenzalida, R., Schneider, W., Garces-Vargas, J., Bravo, L. and Lange, C. (2009) Vertical and horizontal extension of the oxygen minimum zone in the eastern South Pacific Ocean. *Deep-Sea Res. II* **56:**992–1003.

Gilman, E., Zollett, E., Beverly, S. *et al.* (2006) Reducing sea turtle by-catch in pelagic longline fisheries. *Fish and Fisheries* **7:**2–23.

Gilman, E., Kobayashi, D., Swenarton, T., Brothers, N., Dalzell, P. and Kinan-Kelly, I. (2007) Reducing sea turtle interactions in the Hawaii-based longline swordfish fishery. *Biol. Conserv.* **139:**19–28.

Hanan, D.A., Holts, D.B. and Coan, A.L. Jr (1993) The California drift gill net fishery for sharks and swordfish, 1981–82 through 1990–91. *Fish. Bull.* **175:**89–95.

Hinton, M.G. (2003) Status of swordfish stocks in the eastern Pacific ocean estimated using data from Japanese tuna longline fisheries. *J. Mar. Freshw. Res.* **54:**393–399.

HMS SAFE Report(2007) *Stock Assessment and Fishery Evaluation.* Status of the U.S. west coast fisheries for highly migratory species through 2006. PFMC. Portland, OR. pp. 18–32.

Holland, K.N., Brill, R.W., Chang, R.K.C., Sibert, J.R. and Fournier, D. (1992) Physiological and behavioral thermoregulation in bigeye tuna, *Thunnus obesus*. *Nature* **358:**410–412.

Holts, D.B., Bartoo, N.W. and Bedford, D.W. (1994) Swordfish tracking in the Southern California Bight. *U.S. Nat. Mar. Fish. Serv., Southwest Fish. Sci. Center, Admin. Rep.* **LJ No. 94–15:**9p.

Julian, F. and Beeson, M. (1998) Estimates of marine mammal, turtle, and seabird mortality for two California gillnet fisheries: 1990–1995. *Fish. Bull.* **96:**271–284.

Karstensen, J., Stramma, L. and Visbeck, M. (2008) Oxygen minimum zones in the eastern tropical Atlantic and Pacific oceans. *Prog. Oceanogr.* **77:**331–350.

Kringel, K., Jumars, P.A. and Holliday, D.V. (2003) A shallow scattering layer: high-resolution acoustic analysis of nocturnal vertical migration from the seabed. *Limnol. Oceanogr.* **48:**1223–1234.

Levin, L.A. (2003) Oxygen minimum zone benthos: adaptation and community response to hypoxia. *Oceanogr. Mar. Biol. Annu. Rev.* **41:**1–45.

Markaida, U. and Hochberg, F.G. (2005) Cephalopods in the diet of swordfish *Xiphias gladius* Linnaeus caught off the west coast of Baja California, Mexico. *Pac. Sci.* **59:**25–41.

Melvin, E.F., Parrish, J.K. and Conquest, L.L. (1999) Novel tools to reduce seabird bycatch in coastal gillnet fisheries. *Cons. Biol.* **13:**1386–1397.

Musyl, M.K., Brill, R.W., Boggs, C.H., Curran, D.S., Seki, M.P. and Kazama, T.K. (2003) Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts of the Hawaiian Archipelago from archival tagging data. *Fish. Oceanogr.* **12:**152–169.

Pacific Offshore Take Reduction Plan (2008) Take Reduction Plan Regulations and Emergency Regulations. Title 50 *CFR* **229.31** 658–659pp.

Palacios, D.M., Bograd, S.J., Mendelssohn, R. and Schwing, F.B. (2004) Long-term and seasonal trends in stratification in the California Current, 1950–1993. *J. Geophys. Res.*, **109:**C10016. doi:10.1029/2004JC002380

Polovina, J., Balazs, G., Howell, E. and Parker, D. (2003) Dive-depth distribution of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific: might deep longline sets catch fewer turtles? *Fish. Bull.* **101:**189–193.

Prince, E.D. and Goodyear, C.P. (2006) Hypoxia-based habitat compression of tropical pelagic fishes. *Fish. Oceanogr.* **15:**451–464.

Reeb, C.A., Arcangeli, L. and Block, B.A. (2000) Structure and migration corridors in Pacific populations of the Swordfish *Xiphius gladius*, as inferred through analyses of mitochondrial DNA. *Mar. Biol.* **136:**1123–1131.

Sedberry, G.R. and Loefer, J.K. (2001) Satellite telemetry tracking of swordfish, *Xiphias gladius*, off the eastern United States. *Mar. Biol.* **139:**355–360.

Sepulveda, C.A., Kohin, S., Chan, C., Vetter, R. and Graham, J.B. (2004) Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight. *Mar. Biol.* **145:**191–199.

Sinclair, E.H. (1994) Prey of juvenile northern elephant seals (*Mirounga angustirostris*) in the southern California bight. *Mar. Mam. Sci.* **10:**230–239.

Stevens, E.D. and McLeese, J.M. (1984) Why bluefin tuna have warm tummies: temperature effect on trypsin and chymotrypsin. *Am. J. Physiol.* **246:**R487–R494.

Takahashi, M., Okamura, H., Yokawa, K. and Okazaki, M. (2003) Swimming behaviour and migration of a swordfish recorded by an archival tag. *Mar. Freshw. Res.* **54:**527–553.

Uhlmann, S., Fletcher, D. and Moller, H. (2005) Estimating incidental takes of shearwaters in driftnet fisheries: lessons for the conservation of seabirds. *Biol. Cons.* **123:**151–163.

Ward, P. and Meyers, R.A. (2005) Shifts in open-ocean fish communities coinciding with the commencement of commercial fishing. *Ecology* **86:**835–847.

Ward, P., Porter, J.M. and Elscot, S. (2000) Broadbill swordfish: status of established fisheries and lessons for developing fisheries. *Fish and Fisheries* **1:**317–336.

Weng, K.C., O'Sullivan, J.B., Lowe, C.G. III, Winkler, C.E., Dewar, H. and Block, B.A. (2007) Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. *Mar. Ecol. Prog. Ser.* **338:**211–224.