

Volume 21 Issue 7 *Vol 22, Supplemental* 

Article 36

# DIEL OSCILLATIONS IN SAILFISH VERTICAL MOVEMENT BEHAVIOR IN THE EAST CHINA SEA

Wei-Chuan Chiang Eastern Marine Biology Research Center, Fisheries Research Institute, Taitung, Taiwan, R.O.C., wcchiang@mail.tfrin.gov.tw

Ryo Kawabe Graduate School of Fisheries Science and Environmental Studies, Nagasaki University, Nagasaki, Japan.

Michael K. Musyl Pelagic Research Group LLC, Hawaii, USA.

Chi-Lu Sun Institute of Oceanography, National Taiwan University, Taipei, Taiwan, R.O.C.

Hsiao-Min Hung Eastern Marine Biology Research Center, Fisheries Research Institute, Taitung, Taiwan, R.O.C.

See next page for additional authors

Follow this and additional works at: https://jmstt.ntou.edu.tw/journal

Part of the Aquaculture and Fisheries Commons

#### **Recommended Citation**

Chiang, Wei-Chuan; Kawabe, Ryo; Musyl, Michael K.; Sun, Chi-Lu; Hung, Hsiao-Min; Lin, Hsien-Chung; Watanabe, Shun; Furukawa, Seishiro; Chen, Wen-Yie; Chen, Yu-Kai; and Liu, Don-Chung (2013) "DIEL OSCILLATIONS IN SAILFISH VERTICAL MOVEMENT BEHAVIOR IN THE EAST CHINA SEA," *Journal of Marine Science and Technology*: Vol. 21: Iss. 7, Article 36.

DOI: 10.6119/JMST-013-1220-15 Available at: https://imstt.ntou.edu.tw/journal/vol21/iss7/36

This Research Article is brought to you for free and open access by Journal of Marine Science and Technology. It has been accepted for inclusion in Journal of Marine Science and Technology by an authorized editor of Journal of Marine Science and Technology.

## DIEL OSCILLATIONS IN SAILFISH VERTICAL MOVEMENT BEHAVIOR IN THE EAST CHINA SEA

#### Acknowledgements

The authors especially thank Captain Chuen-Min Hsu of the FV Jan-Ji for his skill on catching sailfish. We thank Dr. Chi Him (Tim) Lam, University of University of Massachusetts, for providing help in the use of the sea surface temperature corrected (unscented) Kalman filter. This study was partially financially supported by the Fisheries Research Institute (FRI), Council of Agriculture, Taiwan, and the National Science Council through grants 99AS-10.2.1-W-A1(5) and NSC100- 2914-I-056-001-A1, and by FY2012 Japan Society for Promotion of Science (JSPS) Invitation Fellowship Program for Research in Japan (Short-Term) No. S-12082 to Wei-Chuan Chiang. We would also like to thank for the large-scale oceanographic survey around the island of Taiwan (Taiwan Cooperative Oceanic Fisheries Investigation, TaiCOFI), conducted by the FRI (grant no. 99AS-10.2.1-W-A3).

#### Authors

Wei-Chuan Chiang, Ryo Kawabe, Michael K. Musyl, Chi-Lu Sun, Hsiao-Min Hung, Hsien-Chung Lin, Shun Watanabe, Seishiro Furukawa, Wen-Yie Chen, Yu-Kai Chen, and Don-Chung Liu

### DIEL OSCILLATIONS IN SAILFISH VERTICAL MOVEMENT BEHAVIOR IN THE EAST CHINA SEA

Wei-Chuan Chiang<sup>1</sup>, Ryo Kawabe<sup>2</sup>, Michael K. Musyl<sup>3</sup>, Chi-Lu Sun<sup>4</sup>, Hsiao-Min Hung<sup>1</sup>, Hsien-Chung Lin<sup>1</sup>, Shun Watanabe<sup>2</sup>, Seishiro Furukawa<sup>2</sup>, Wen-Yie Chen<sup>1</sup>, Yu-Kai Chen<sup>5</sup>, and Don-Chung Liu<sup>5</sup>

Key words: diel diving, pop-up satellite archival tag, mixed-layer depth, temperature threshold.

#### ABSTRACT

A sailfish (Istiophorus platypterus) was tagged with a pop-up satellite archival tag off the eastern coast of Taiwan and moved in a northerly direction to the East China Sea, where the tag popped-up after 160 days. The total linear displacement was 550 km from deployment to pop-up location and all movements were confined to the East China Sea. After the primarily southward movement during first two months at-liberty, the sailfish changed course after September and began to swim in a northerly direction paralleling the Kuroshio Current. During these horizontal movements, the tagged animal exhibited diel oscillations in its vertical diving behavior. On 22 days of the entire 160 days-at-liberty, the sailfish dove to depths deeper than 100 m. The sailfish spent >85% of its time in the upper uniformly mixed layer above ~50 m, but made more extensive vertical movements during the daytime ( $\overline{x} = 32.2 \text{ m} \pm 34.5 \text{ SD}$ ) than nighttime ( $\overline{x} = 9.5$  $m \pm 16.7$  SD). Depths and ambient water temperatures visited ranged from 0 to 153 m and 29.7°C to 17.8°C, respectively. The depth distribution appeared to be limited by ~6°C to 8°C changes in water temperature (Delta T) relative to sea surface temperature.

#### I. INTRODUCTION

An increasing body of evidence suggests that overexploitation threatens the sustainable use of many of the world's large apex predatory fishes [22, 15]. Gathering information on movements and behavior of large vagile predators is challenging. The time and the expense required to locate and monitor billfish over large geographic areas is often prohibitive. It has been suggested that physiological attributes, foraging behavior, and environmental conditions predominantly influence how billfish utilize vertical habitat [6, 35]. In turn, behavioral adaptations resulting from physiological responses to oceanographic conditions are likely to affect vulnerability to fishing gear [36]. Development of pop-up satellite archival tag (PSAT) technology has greatly increased our knowledge of billfishes [1]. PSAT technology established an effective fisheries independent method to monitor ambient depth (pressure), temperature, and light levels on tags attached to animals for extended periods [1, 4]. PSATs can offer many benefits to study vertical dive behavior, as well as providing information on migration routes, possible spawning areas, exchange rates between areas and post-release mortality [32].

Studies have indicated that billfish spend most of their time in the warmer surface mixed layer above the thermocline [20, 21], with sailfish usually exhibiting a greater affinity for nearsurface depths over continental shelves compared to other istiophorids [10, 25, 37]. Cardiac temperature threshold and dissolved oxygen concentrations are thought to be major factors restricting the vertical habitat of istiophorids. Changes in water temperature relative to the surface temperature (Delta T), rather than any particular temperature, limits their vertical mobility [6, 20]. Istiophorids have physiological adaptations (e.g., brain heaters, enhanced photoreceptors) that allow for brief excursions into deeper strata having lower temperatures and poor visibility [5, 19]. The cold hypoxic environment below the thermocline has been reported to limited vertical habitat use of istiophorids [35, 36] and Stramma et al. [40] indicated expansion of oxygen minimum zones may reduce

Paper submitted 11/03/13; revised 12/04/13; accepted 12/20/13. Author for correspondence: Wei-Chuan Chiang (e-mail: wcchiang@mail.tfrin.gov.tw).

<sup>&</sup>lt;sup>1</sup>Eastern Marine Biology Research Center, Fisheries Research Institute, Taitung, Taiwan, R.O.C.

<sup>&</sup>lt;sup>2</sup> Graduate School of Fisheries Science and Environmental Studies, Nagasaki University, Nagasaki, Japan.

<sup>&</sup>lt;sup>3</sup> Pelagic Research Group LLC, Hawaii, USA.

<sup>&</sup>lt;sup>4</sup> Institute of Oceanography, National Taiwan University, Taipei, Taiwan, R.O.C.

<sup>&</sup>lt;sup>5</sup> Fisheries Research Institute, Keelung, Taiwan, R.O.C.

available habitat for other tropical pelagic fishes. Understanding depth distributions is useful for predicting vulnerability to fishing gears and improving estimates of relative abundance derived from catch rate indices.

The biology, ecology and stock status of sailfish has been investigated in eastern Taiwan [11-13]. Chiang *et al.* [10] reported movements of PSAT tagged sailfish in eastern Taiwan and movement information was based on short-term deployments of sailfish to characterize vertical habitat to provide information to improve stock assessments. Longer PSAT retention times will be needed to investigate movements in the context of climate variability. The impacts of environmental change on the behavior of billfish in the East China Sea are largely unknown. The objectives of our study were to examine the long-term movement patterns, and to characterize the oceanographic and thermal habitat preferences of sailfish in East China Sea using PSATs.

#### **II. MATERIAL AND METHODS**

A sailfish (Istiophorus platypterus) (~230 cm LJFL) was captured in eastern Taiwan at 09:40 on 8 July 2010 at 23.070°N; 121.34°E using commercial longline gear targeting dolphinfish (Coryphaena hippurus). Round weight was estimated by the captain, and lower jaw fork length was derived from length-weight regressions [16]. Deployment of longline sets occurred before dawn (depths of ~0 to 45 m) and 6 m monofilament gangions were baited with squid sticks (Loglio spp.) and live milkfish (Chanos chanos). After being gently leadered to the side of the vessel, a PSAT (model x-tag, Microwave Telemetry, Columbia, MD) was attached at the base of dorsal fin using a 2m pole. The fish did not appear to be injured from the process of capture, tag and release. The tag was programmed to pop-up on 8 February 2011. The J hook was removed prior to release. The tagging procedure was completed in approximately 1 minute.

The tag head, tether and applicator tip were liberally bathed in Betadine solution (10% solution of povidone–iodine) and then immediately inserted near the base of the dorsal fin between spaces of the interneural and neural spines. The tether was made of ~123 kg fluorocarbon with stainless steel crimps matching the diameter of the line and a stainless steel ball bearing (Sampo no. 6, Barneveld, NY, USA) was placed ~10 cm from the tag head and to reduce torque and precession [32]. Surgical grade nylon tag heads were augmented with speargun 'flopper blades' to increase surface area. PSAT and tether/tag head combinations were positively buoyant in water. The locations of tagging event was recorded using GPS.

Depth and temperature data were measured in the PSAT as 8-bit numbers, yielding a depth resolution of 0.34~5.4 m and temperature resolution of 0.16~0.23°C. Fail-safe options were programmed into the tag where stationary PSATs (i.e., those experiencing no significant changes in pressure) or shed tags would begin to transmit archived data to the Argos satellite system after four days. In the event of mortality, once the fish sank to ~1200 m and remained for ~15 minutes, the PSAT would separate from the fish, float to the surface, and begin transmitting stored data to Argos. After pop off, the tag relayed archived data via Argos, including daily maximum depths, archived pressure (depth) temperature readings, and raw light-based geolocations (http://www.microwavetelemetry. com/fish/popupTag.cfm). We subsequently applied a sea surface temperature (SST) corrected (unscented) Kalman filter [31] to calculate most probable tracks (MPTs) from the raw geolocations. The linear displacements from tagging to pop-up locations were determined using the Great Circle Distance and release locations were estimated by Doppler shift. Only Argos messages with location classes of 1 or higher were used to determine pop-up locations.

Depth and temperature data were assigned to daytime or nighttime periods by calculating times of local dawn and dusk of the MPTs from http://aa.usno.navy. mil/. To further explore daytime and nighttime differences in the data, we used onesample Kolmogorov-Smirnov tests to compare distributions of ambient temperature (day, night, combined) and depth (day, night, combined) data to that of a normal distribution and all tests indicated that data distributions were non normally distributed (P < 0.01). Next, a non-parametric Runs test indicated the depth and temperature time series data were randomly distributed. Therefore, we used non-parametric twosample Kolmogorov-Smirnov tests to compare daytime and nighttime temperature and depth preferences, and Mann-Whitney W-tests to compare differences in medians between daytime and nighttime data for depth and temperature [41].

Time-at-depth and time-at-temperature data were aggregated into 10-m and 1°C bins, respectively. These data were subsequently expressed as a fraction of the total time of observation for sailfish. The P < 0.05 level was taken to indicate statistical significance. Oceanographic habitat was characterized using the data from the Taiwan Cooperative Oceanic Fisheries Investigation (TaiCOFI) from The Fishery Research I September 2010 cruise at sampling stations [18] encompassing the MPT. Temperature and salinity at different depths were obtained by a SeaBird conductivity-temperature-depth (CTD) instrument lowered from the surface to a depth of 1000 m and were compared to vertical data from tagged sailfish. Dissolved oxygen (DO) concentrations were obtained from NODC (National Oceanographic Data Center) (http://www.nodc.noaa.gov/).

#### III. RESULTS

After 160 days-at-liberty, the tag popped up prematurely on 15 December 2010 at 26.866°N; 125.676°E in East China Sea, ~200 km from eastern Okinawa. The linear displacement was 550 km from deployment to pop-up location and all the movements were confined to the East China Sea (Fig. 1). After the first 116 days of primarily southward movement, the sailfish changed course and began to swim northerly during September (Fig. 2).

We obtained a total of 144 days of depth and temperature



Fig. 1. Deployment (●), pop-up location (★) and most probable track calculated from the KFSST for sailfish (~230 cm LJFL) carrying PSAT and hatched area encompasses the 95%CI.; data received, 160 days.



Fig. 2. Percentage of time spent in individual depth strata (top panel) and temperature strata (bottom panel) for sailfish.

data. The mean depth occupied was 21.3 m (±29.7 SD, range: 0 to 153 m) and the mean temperature occupied was 26.2°C (±2.4 SD, range: 17.8°C to 29.7°C). The sailfish spent ~58% of its time above 10 m (~43% during the day and ~73% during the night) and exhibited greater variability near crepuscular times with more extensive vertical movements during daytime. The sailfish spent >85% of its time in the upper uniform mixed layer above ~50 m in water  $\geq 25^{\circ}$ C (~72% during the day and ~98% during the night, Fig. 3), but made more extensive vertical movements during the daytime ( $\bar{x} = 32.2 \text{ m} \pm 34.5 \text{ SD}$ ) than nighttime ( $\bar{x} = 9.5 \text{ m} \pm 16.7 \text{ SD}$ ). Depths and ambient water temperatures visited ranged from 0 to 153 m and 29.7°C to 17.8°C, respectively. On 22 days



Fig. 3. Temperature-depth profiles obtained from the aggregated data from this study and Chiang *et al.* [10].

of the entire 160 days-at-liberty, the sailfish dived to depths deeper than 100 m. During the day, however, it show a tendency to visit both shallower ( $0 \sim 50$  m) and deeper strata ( $100 \sim 150$  m) than during the night when it spent most of its time between surface to 50 m. At night, the fish rarely descended >60 m.

Based on temperature-depth profiles collected by the PSAT, ~25°C isotherm corresponded to depth ~120 m (Fig. 3) and the bottom of the mixed-layer (MLD) appears to be ~100-150 m (Fig. 4). Diel episodes of diving behavior was recorded throughout the entire track (Fig. 4) and the fish experienced cooler water temperatures during repeated deep diving in day time. Minimum temperature, SST and maximum dive periods are shown in Fig. 5 and it is obvious that sailfish spend the majority of their time in the uniform temperature surface layer and vertical movements appeared to be limited by a temperature change of  $\leq 8^{\circ}$ C (Table 1). The Delta T percentages pooled indicated that about 51% of day time, and 85% night time were spent at or near the surface (i.e. Delta T =0 and 1; Table 1). Kruskal-Wallis one-way ANOVAs to test for differences between medians, and all Kolmogorov Smirnov comparisons were significantly different between months (Fig. 6), day and night for depth and temperature data.

Data from the CTD probe indicated the mixed layer was at 70~100 m, and thermocline extended beyond 500 m where temperatures were <10°C (Fig. 7). From the surface to 75 m, salinities ranged from 34.41 to 34.80‰, and the oxygen concentration was ~4.5 mg  $I^{-1}$ , with an extended oxycline to ~200 m where the concentrations reached 4 mg  $I^{-1}$ .

#### **IV. DISCUSSION**

#### 1. Habitat Preference

The environmental preferences of sailfish define the vertical niche of the species, and thereby its relationship with other predators and prey in the pelagic environment. Tagged sailfish

Fish

Time



Fig. 4. Depth records for sailfish. Depth record covering 160 days at liberty (top panel), 4-day (middle panel) and 1-day (bottom panel) period during which the fish showed the characteristic vertical movement patterns with dawn and dusk transitions. The grey horizontal bars indicate nighttime.



Fig. 5. Minimum temperature (min temp), SST and maximum depth (max depth) for sailfish.

Table 1. Cumulative percentage of temperature readings from pop-up satellite archival tags (PSATs) attached to sailfish expressed as differences from daily mean sea surface temperature ( $\Delta$ SST). SST was calculated as per and is analogous to surface layer [8, 34]. Sailfish\*, Sailfish\*\* and Sailfish\*\*\* were data published at Chiang et al. [10].

 $\Delta$ SST (°C)

1 1511	THIE	0	-1	-2	-3	-4	-5	-6	-7	<-8
	Day	7.49	50.75	61.73	72.55	78.70	84.36	90.52	95.01	97.67
Sailfish	Night	18.50	82.00	90.67	93.50	95.67	97.17	98.17	99.00	99.33
	Total	12.99	66.36	76.19	83.01	87.18	90.76	94.34	97.00	98.50
	Day	37.33	79.00	88.5	94.83	97.17	98.83	99.67	100	100
Sailfish*	Night	26.03	66.62	80.15	87.5	91.62	95.29	97.36	99.56	100
G 110 1 44	Total	31.68	72.81	84.33	91.17	94.4	97.06	98.52	99.78	100
Sailfish**	Total	28.57	61.07	77.50	89.29	94.29	96.79	97.86	98.93	100
Sailfish***	Total	19.85	47.55	63.48	74.26	82.11	85.54	87.75	88.97	90.44
31 14 12 13 10 10 10 10 0 0 0 0 0 0	80 - 60 - 40 - 20 - 80 - 80 - 40 -	A	Ţ						]	
2	20 -	白		, E		F		_ L_		
	0		Ţ-			_				
		Jul	Aug	g S	ep	Oct	Nov	Dec	2	
	35	В								
3	30 -	-	Ŧ							
Temperature (°C)	25 - 20 -						Ī	Ī	3	
L '						Ŧ				
1	15 -									
	1.0									
]	10 +	Jul	Aug	g S	ep Mont	Oct h	Nov	Dec	c	•

Fig. 6. Box plots of depth (A) and temperature (B) for sailfish in the waters off eastern Taiwan tracking area during July to December 2010. The centerline represents the median and the boxes represent 95%CI. The whiskers extend the maximum and minimum. Horizontal lines indicate the ranges.



Fig. 7. Temperature profile from a conductivity, temperature and depth recorder (CTD; red line) from research cruise of the *Fishery Researcher I* (FR1-201009), and the oxygen profile (black line) around tracking area at September from NOAA National Oceanographic Data Center (http://www.nodc.noaa.gov).

in the present report made similar horizontal and vertical movements in the East China Sea to what Chiang et al. [10] reported. In both studies sailfish spent most time from 0 to 50 m depth. The present study examined data over five month period encompassing summer, autumn and early winter and is the longest reported retention for a PSAT on a sailfish [10, 26]. The time spent in various temperature strata indicate that sailfish in the East China Sea have generally a preference for warmer near-surface depths than other istiophorid billfish [16, 17, 21, 39]. The Kuroshio current enters the East China Sea through the strait between Taiwan and Yonakunijima Island, the easternmost island of the Ryuku Islands [30], and generates a convergence zone at the boundary between the Kuroshio current and a countercurrent system produced by bottom shelf water [1]. In winter time, the cold and low salinity Chinese Coastal Water go southerly [30] and may cause the sailfish stay at southern boundary of the East China Sea. From the wind data in Comprehensive Ocean-Atmosphere Data Set (COADS), there is seasonal variation of the monsoon winds [14]. In summer, weak southeast winds prevail, and the sailfish may have been assisted by the wind during northern excursions. In winter time, the strong northwest winds prevail, influencing the sailfish to stay at the southern East China Sea.

#### 2. Diving Behavior

The depth distribution of sailfish is probably associated with ambient water temperature as has been shown for other pelagic fish species in a variety of electronic tagging studies [6, 16, 27]. The cooler water temperatures encountered by the fish at daytime on deep dives were probably related to foraging or perhaps avoiding predators.

Billfish are visual feeders, and they must limit foraging

activities to periods with adequate visibility. Variability in vertical excursions is often associated with billfish foraging, predator avoidance, removal of parasites, or as an aid to orientation/navigation [33, 38]. In turn, spending as much time as possible in warmer surface temperatures during periods of decreased activity (darkness) may serve as an energy-saving opportunity [26]. Given that adequate dissolved oxygen is available, istiophorid billfishes prefer the warmest water available and that the change in water temperature rather than a specific temperature is what governs vertical distribution [8].

Prince *et al.* [35] described how the vertical habitat distribution of Atlantic and Pacific sailfish and blue marlin were directly correlated with DO, and that hypoxic layers formed barriers to limit vertical movements. Limited data on DO concentrations in our study area could not confirm nor refute whether oxygen was a limiting factor on vertical diving patterns but we suspect it was not. At the depths routinely visited, the vertical distribution of sailfish appeared to be limited by temperature gradients [25, 28].

Sailfish exhibit diel vertical movements, characteristic of other billfishes [8, 24]. In daytime, the greatest percentage of time was spent near the surface which we interpret as basking behavior similar to that of swordfish [9]. PSAT and ultrasonic tracking studies on sailfish show 84% of their time was spent in the upper 10 m [25, 26, 28, 37]. Tracking studies on other istiophorid billfish in different parts of the world, where regional oceanography and thermal structure are clearly different, suggests a common overall preference for the uniform surface mixed layer [21, 25, 29], but the reasons for this preference are not fully understood. The large proportion of time sailfish spend near the surface, however, results in an increased vulnerability to entanglement in gillnets and other surface gears.

#### 3. Temperature Threshold

The tagged sailfish does not appear to respond directly to depth but rather to vertical temperature structure. Due to cardiac temperature thresholds that limit the ability of istiophorids to endure cold extremes over extended periods [8], the maximum Delta T visited is usually no more than 8°C below the surface temperature. Sailfish spent <1% of their time in strata colder than 8°C [26], and exhibited less individual variability in overall vertical habitat use compared to the more stochastic and complex behavior described for blue marlin [20]. Both sailfish and blue marlin are cold-blooded, but they do possess brain and eye heater tissue that support functionality of these organs as ambient temperatures decrease [5].

For tagged sailfish, a recurrent theme suggests they exhibit characteristic diel diving patterns found in other billfish species. Although daytime and nighttime diving transitions were not as pronounced as found in other pelagic fishes, tagged sailfish exhibited deeper (and more variable) diving excursions at day time presumably when the animals were foraging. In daytime, the greatest percentage time was spent near the



Fig. 8. Isopleths of dissolved oxygen at 150 m depth around this study tracking area during July to December 2010.

surface which we interpret as basking behavior which correlates with anecdotal information. While sailfish has been tracked in water temperature from  $17.8^{\circ}$ C to  $29.7^{\circ}$ C, temperature change during single dives are usually restricted by  $8^{\circ}$ C and  $6^{\circ}$ C changes in water temperature (Delta T) relative to sea surface temperature.

Combined with the data with Chiang *et al.* [10] for the same study area, Table 1 shows the pooled Delta T values for day and night. This information is important and serves as a metric that can be applied directly to regional habitat standardization models [3, 23] to facilitate predictions for vertical distribution and relative abundance of sailfish. The behavioural plasticity shown by this sailfish is similar to other pelagic fishes, sharks and turtles, which display diving and diel vertical migrations to match behaviour of their prey probably by optimizing their searching strategy (to the extent of the physiological limitations of themselves and their prey).

Tropical pelagic fishes do not have the tolerance to hypoxia [5, 40], and oxygen is a critical factor in the habitat available to sailfish. In the present study, sailfish spent >85% of their time in waters shallower than 50 m, which corresponded to the mixed layer above the oxycline (Fig. 7). Below this depth, dissolved oxygen declined from values  $<4.5 \text{ mg l}^{-1}$  to  $\sim4 \text{ mg l}^{-1}$ (Fig. 8). The geographic range and diving behaviour of sailfish may be related to thermal effects on cardiac performance. Detailed knowledge of behavior, physiology and habitat enables fishing techniques to be tailored to target particular species more accurately [6]. In the East China Sea, sailfish are taken as by-catch in the longline and coastal fishery. By examining sailfish vertical mobility and habitat, the data presented in this paper provides a foundation for research into ways to reduce sailfish by-catch in longline and coastal fishery. This study presented the longest retention period for PSATs carried by sailfish in the East China Sea and underscores the importance of continual tagging experiments.

#### ACKNOWLEDGMENTS

The authors especially thank Captain Chuen-Min Hsu of the FV Jan-Ji for his skill on catching sailfish. We thank Dr. Chi Him (Tim) Lam, University of University of Massachusetts, for providing help in the use of the sea surface temperature corrected (unscented) Kalman filter. This study was partially financially supported by the Fisheries Research Institute (FRI), Council of Agriculture, Taiwan, and the National Science Council through grants 99AS-10.2.1-W-A1(5) and NSC100-2914-I-056-001-A1, and by FY2012 Japan Society for Pro-

motion of Science (JSPS) Invitation Fellowship Program for Research in Japan (Short-Term) No. S-12082 to Wei-Chuan Chiang. We would also like to thank for the large-scale oceanographic survey around the island of Taiwan (Taiwan Cooperative Oceanic Fisheries Investigation, TaiCOFI), conducted by the FRI (grant no. 99AS-10.2.1-W-A3).

#### REFERENCES

- Andres, M., Wimbush, M., Park, J. H., Chang, K. I., Lim, B. H., Watts, D. R., Ichikawa, H., and Teague, W. J., "Observations of Kuroshio flow variations in the East China Sea," *Journal of Geophysical Research*, Vol. 113 (C05013), pp. 1-14 (2008).
- Arnold, G. and Dewar, H., "Electronic tags in marine fisheries research," in: Sibert, J. R. and Nielsen, J. L. (Eds.), *Tagging and Tracking Marine Fish with Electronic Devices*, University of Hawaii, East-West Center, Kluwer Academic, pp. 7-64 (2001).
- Bigelow, K. A., Hampton, J., and Miyabe, N., "Application of a habitat-based model to estimate effective longline fishing effort and relative abundance of Pacific bigeye tuna (*Thunnus obesus*)," *Fisheries Oceanography*, Vol. 11, pp. 143-155 (2002).
- Block, B. A., Dewar, H., Farwell, C., and Prince, E. D., "A new satellite technology for tracking the movements of Atlantic bluefin tuna," *Proceedings of the National Academy of Sciences*, Vol. 95, pp. 9384-9889 (1998).
- Block, B. A., "Structure of the brain and eye heater tissue in marlins, sailfish, and spearfishes," *Journal of Morphology*, Vol. 190, pp. 169-189 (1986).
- Brill, R. W. and Lutcavage, M., "Understanding environmental influences on movements and depth distributions of tunas and billfishes can significantly improve population assessments," *American Fisheries Society Symposium*, Vol. 25, pp.179-198 (2001).
- Brill, R. W., Holts, D. B., Chang, R. K. C., Sullivan, S., Dewar, H., and Carey, F. G., "Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurement of oceanic currents," *Marine Biology*, Vol. 117, pp. 567-574 (1993).
- Brill, R. W., Block, B. A., Boggs, C. H., Bigelow, K. A., Freund, E. V., and Marcinek, D. J., "Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes," *Marine Biology*, Vol. 133, pp. 395-408 (1999).
- Carey, F. G. and Robinson, B. H., "Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry," *Fishery Bulletin*, Vol. 79, pp. 277-292 (1981).
- Chiang, W. C., Musyl, M. K., Sun, C. L., Chen, S. Y., Chen, W. Y., Liu, D. C., Su, W. C., Yeh, S. Z., Fu, S. C., and Huang, T. L., "Vertical and horizontal movements of sailfish (*Istiophorus platypterus*) near Taiwan determined using pop-up satellite tags," *Journal of Experimental Marine Biology and Ecology*, Vol. 397, pp. 129-135 (2011).
- Chiang, W. C., Sun, C. L., Yeh, S. Z., and Su, W. C., "Age and growth of sailfish (*Istiophorus platypterus*) in waters off eastern Taiwan," *Fishery Bulletin*, Vol. 102, pp. 251-263 (2004).
- Chiang, W. C., Sun, C. L., Yeh, S. Z., Su, W. C., and Liu, D. C., "Spawning frequency and batch fecundity of the sailfish (*Istiophorus platypterus*) (Istiophoridae) in waters off eastern Taiwan," *Zoological Studies*, Vol. 45, pp. 483-490 (2006).
- Chiang, W. C., Chen, Y., Sun, C. L., Su, W. C., Wang, S. P., Liu, D. C., Yeh, S. Z., and Chen, W. Y., "Analysis of sex-specific spawning biomass per recruit of the sailfish (*Istiophorus platypterus*) in the waters off eastern Taiwan," *Fishery Bulletin*, Vol. 107, pp. 265-277 (2009).
- Chu, P., Chen, Y., and Kuninaka, A., "Seasonal variability of the Yellow Sea/East China Sea surface fluxes and thermohaline structure," *Advances in Atmospheric Science*, Vol. 22, pp. 1-20 (2005).

- Collette, B. B., Carpenter, K. E., Polidoro, B. A., Juan-Jordá, M. J., Boustany, A., Die, D. J., Elfes, C., Fox, W., Graves, J., Harrison, L. R., McManus, R., Minte-Vera, C. V., Nelson, R., Restrepo, V., Schratwieser, J., Sun, C. L., Amorim, A., Peres, M. B., Canales, C., Cardenas, G., Chang, S. K., Chiang, W. C., N. de Oliveira Leite, J., Harwell, H., Lessa, R., Fredou, F. L., Oxenford, H. A., Serra, R., Shao, K. T., Sumaila, R., Wang, S. P., Watson, R., and Yáñez, E., "High value and long life - double jeopardy for tunas and billfishes," *Science*, Vol. 333, pp. 291-292 (2011).
- Dewar, H., Prince, E. D., Musyl, M. K., Brill, R. W., Sepulveda, C., Luo, J., Foley, D., Orbesen, E. S., Domeier, M. L., Nasby-Lucas, N., Snodgrass, D., Michael Laurs, R., Hoolihan, J. P., Block, B. A., and McNaughton, L. M., "Movements and behaviors of swordfish in the Atlantic and Pacific Oceans examined using pop-up satellite archival tags," *Fisheries Oceanography*, Vol. 20, pp. 219-241 (2011).
- Domeier, M. L., "An analysis of Pacific striped Marlin (*Tetrapturus audax*) horizontal movement patterns using pop-up satellite archival tags," *Bulletin of Marine Science*, Vol. 79, pp. 811-825 (2006).
- FRI, Cruise Report of TaiCOFI Surveys in 2010, Fisheries Research Institute, Keelung, Taiwan (2011).
- Fritsches, K. A., Marshall, N. J., and Warrant, E. J., "Retinal specializations in the blue marlin: eyes designed for sensitivity to low light levels," *Marine and Freshwater Research*, Vol. 54, pp. 333-341 (2003).
- Goodyear, C. P., Luo, J., Prince, E. D., Hoolihan, J. P., Snodgrass, D., Orbesen, E. S., and Serafy, J. E., "Vertical habitat use of Atlantic blue marlin *Makaira nigricans*: interaction with pelagic longline gear," *Marine Ecology Progress Series*, Vol. 365, pp. 233-245 (2008).
- Gunn, J. S., Patterson, T. A., and Pepperell, J. G., "Short-term movement and behaviour of black marlin *Makaira indica* in the Coral Sea as determined through a pop-up satellite archival tagging experiment," *Marine* and Freshwater Research, Vol. 54, pp. 515-525 (2003).
- Hilborn, R., Branch, T. A., Ernst, B., Scheuerell, M. D., and Valero, J. L., "State of the world's fisheries," *Annual Review of Environment and Resources*, Vol. 28, pp. 359-399 (2003).
- 23. Hinton, M. G. and Nakano, H., "Standardizing catch and effort statistics using physiological, ecological, or behavioral constraints and environmental data, with an application to blue marlin (*Makaira nigricans*) catch and effort data from Japanese longline fisheries in the Pacific," *InterAmerican Tropical Tuna Commission Bulletin*, Vol. 21, pp. 171-200 (1996).
- Holland, K. N., Brill, R. W., and Chang, R. K. C., "Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear," *Fishery Bulletin*, Vol. 88, pp. 397-402 (1990).
- Hoolihan, J. P. and Luo, J., "Determining summer residence status and vertical habitat use of sailfish (*Istiophorus platypterus*) in the Arabian Gulf," *ICES Journal of Marine Science*, Vol. 64, pp. 1791-1799 (2007).
- 26. Hoolihan, J. P., Luo, J., Goodyear, C. P., Orbesen, E. S., and Prince, E. D., "Vertical habitat use of sailfish (*Istiophorus platypterus*) in the Atlantic and eastern Pacific, derived from pop-up satellite archival tag data," *Fisheries Oceanography*, Vol. 20, pp. 192-205 (2011).
- Hoolihan, J. P., Luo, J., Abascal, F. J., Campana, S. E., De Metrio, G., Dewar, H., Domeier, M. L., Howey, L. A., Lutcavage, M. E., Musyl, M. K., Neilson, J. D., Orbesen, E. S., Prince, E. D., and Rooker, J. R., "Evaluating post-release behaviour modification in large pelagic fish deployed with pop-up satellite archival tags," *ICES Journal of Marine*

Science, Vol. 68, pp. 880-889 (2011).

- Hoolihan, J. P., "Horizontal and vertical movements of sailfish (*Istio-phorus platypterus*) in the Arabian Gulf, determined by ultrasonic and pop-up satellite tagging," *Marine Biology*, Vol. 146, pp. 1015-1029 (2005).
- 29. Horodysky, A. Z., Kerstetter, D. W., Latour, R. J., and Graves, J. E., "Habitat utilization and vertical movements of white marlin (*Tetrapturus albidus*) released from commercial and recreational fishing gears in the western North Atlantic Ocean: inferences from short duration pop-up archival satellite tags," *Fisheries Oceanography*, Vol. 16, pp. 240-256 (2007).
- Ichikawa, H. and Beardsley, R. C., "The Current System in the Yellow and East China Seas," *Journal of Oceanography*, Vol. 58, pp. 77-92 (2002).
- Lam, C. H., Nielsen, A., and Sibert, J. R., "Improving light and temperature based geolocation by unscented Kalman filtering," *Fisheries Research*, Vol. 91, pp. 15-25 (2008).
- 32. Musyl, M. K., Domeier, M. L., Nasby-Lucas, N., Brill, R. W., McNaughton, L. M., Swimmer, J. Y., Lutcavage, M. S., Wilson, S. G., Galuardi, B., and Liddle, J. B., "Performance of pop-up satellite archival tags," *Marine Ecology Progress Series*, Vol. 433, pp. 1-28 (2011).
- 33. Musyl, M. K., Brill, R. W., Boggs, C. H., Curran, D. S., Kazama, T. K., and Seki, M. P., "Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data," *Fisheries Oceanography*, Vol. 12, pp. 152-169 (2003).
- Nielsen, A., Bigelow, K. A., Musyl, M. K., and Sibert, J. R., "Improving light-based geolocation by including sea surface temperature," *Fisheries Oceanography*, Vol. 5, pp. 314-325 (2006).
- Prince, E. D. and Goodyear, C. P., "Hypoxia-based habitat compression of tropical pelagic fishes," *Fisheries Oceanography*, Vol. 15, pp. 451-464 (2006).
- Prince, E. D., Luo, J., Phillip Goodyear, C., Hoolihan, J. P., Snodgrass, D., Orbesen, E. S., Serafy, J. E., Ortiz, M., and Schirripa, M. J., "Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes," *Fisheries Oceanography*, Vol. 19, pp. 448-462 (2010).
- 37. Prince, E. D., Holts, D. B., Snodgrass, D., Orbesen, E. S., Luo, J., Domeier, M. L., and Serafy, J. E., "Transboundary movement of sailfish, *Istiophorus platypterus*, off the Pacific coast of central America," *Bulletin* of Marine Science, Vol. 79, pp. 827-838 (2006).
- 38. Sims, D. W., Southall, E. J., Humphries, N. E., Hays, G. C., Bradshaw, C. J. A., Pitchford, J. W., James, A., Ahmed, M. Z., Brierley, A. S., Hindell, M. A., Morritt, D., Musyl, M. K., Righton, D., Shepard, E. L. C., Wearmouth, V. J., Wilson, R. P., Witt, M. J., and Metcalfe, J. D., "Scaling laws of marine predator search behaviour," *Nature*, Vol. 451, pp. 1098-1102 (2008).
- 39. Sippel, T. J., Davie, P. S., Holdsworth, J. C., and Block, B. A., "Striped marlin (*Tetrapturus audax*) movements and habitat utilization during a summer and autumn in the Southwest Pacific Ocean," *Fisheries Ocean*ography, Vol. 16, pp. 459-472 (2007).
- 40. Stramma, L., Prince, E. D., Schmidtko, S., Luo, J., Hoolihan, J. P., Visbeck, M., Wallace, D. W. R., Brandt, P., and Körtzinger, A., "Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes," *Nature Climate Change*, Vol. 2, pp. 33-37 (2011).
- 41. Zar, J. H., Biostatistical Analysis, Prentice Hall, New Jersey, USA (1996).