

*Diel vertical movements of adult male  
dolphinfish (Coryphaena hippurus) in the  
western central Atlantic as determined by  
use of pop-up satellite archival transmitters*

**Wessley Merten, Richard Appeldoorn,  
Roberto Rivera & Donald Hammond**

**Marine Biology**

International Journal on Life in Oceans  
and Coastal Waters

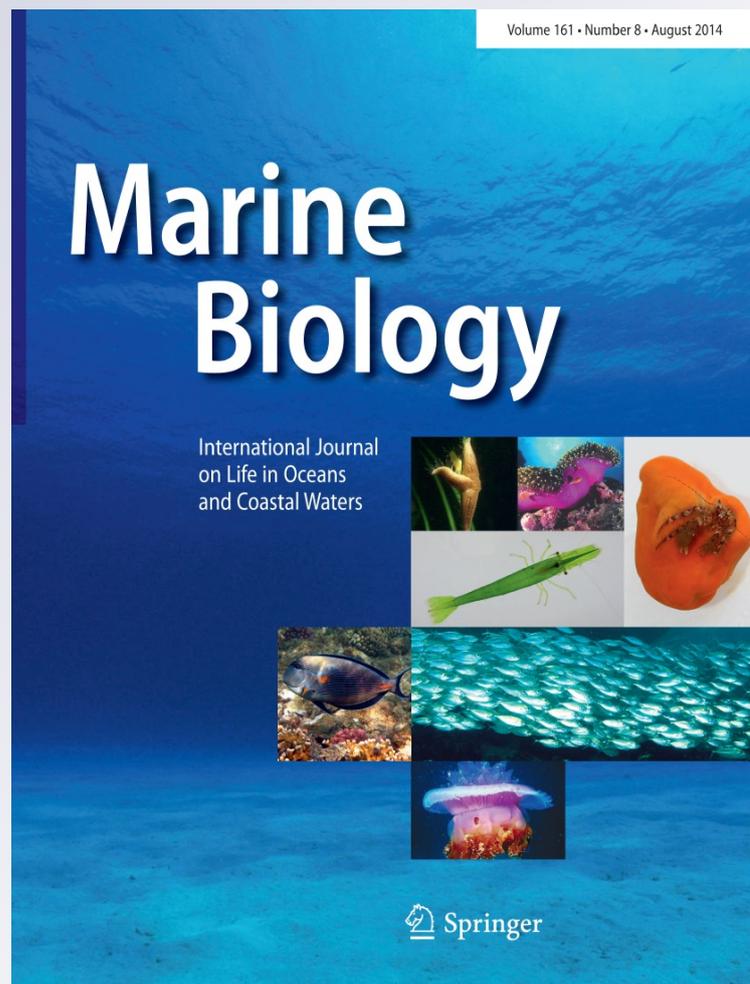
ISSN 0025-3162

Volume 161

Number 8

Mar Biol (2014) 161:1823-1834

DOI 10.1007/s00227-014-2464-0



**Your article is protected by copyright and all rights are held exclusively by Springer-Verlag Berlin Heidelberg. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

# Diel vertical movements of adult male dolphinfish (*Coryphaena hippurus*) in the western central Atlantic as determined by use of pop-up satellite archival transmitters

Wessley Merten · Richard Appeldoorn ·  
Roberto Rivera · Donald Hammond

Received: 4 February 2014 / Accepted: 14 May 2014 / Published online: 7 June 2014  
© Springer-Verlag Berlin Heidelberg 2014

**Abstract** The vertical movements of six adult male dolphinfish (*Coryphaena hippurus*) (95–120 cm estimated fork length), caught using standard sportfishing methods, were investigated using high-rate single-point pop-up satellite archival transmitters from 2005 to 2011 in the western central Atlantic. Data revealed a diel activity pattern within the mixed surface layer with dives below the thermocline suggesting temperature is not a barrier to vertical movements for short periods of time. Dolphinfish were tracked for periods of 4.96–30.24 day ( $\Sigma = 83.37$  day), reaching depths >200 m, and in temperatures ranging from 16.20 to 30.87 °C. The six tags allowed comprehensive vertical movement analyses by time of day, duration at depth, and based on vertical movement patterns. The longest (>60 min), deepest (>30 m), and most extensive vertical movement patterns occurred during night rather than day, with the most time spent near the surface during the day. Dolphinfish spent 66 % of their time in the surface layer (0–9.9 m) and only one individual spent 8 % of the

monitoring period diving >8 °C from the maximum surface temperatures recorded while tracked. Two tags were analyzed based on lunar phase and revealed contrasting relationships between vertical movements during new and full phases. Our results suggest dolphinfish vertically shift between surface and at-depth feeding strategies to exploit aggregating epipelagic and mesopelagic prey items leading to predictable diel vertical movements.

## Introduction

The dolphinfish (*Coryphaena hippurus*) is a large pelagic predator of significant economic importance to commercial and sportfishing industries and artisanal fisheries worldwide (Oxenford and Hunte 1986). In the western central Atlantic, dolphinfish are known to school and associate with drifting objects such as holopelagic algae (*Sargassum* spp.) and flotsam (Hemphill 2005) from George's Bank to Rio de Janeiro, Brazil (Oxenford and Hunte 1983). Throughout this range, dolphinfish undertake long-distance movements at times exceeding 1,000 km along the US east coast (Merten et al. 2014a) and to the Caribbean Sea (Merten et al. 2014b).

Dolphinfish, like wahoo and marlin, are generally observed along continental shelf breaks, deep seamounts, or open ocean temperature and current fronts (Oxenford et al. 2003; Hemphill 2005; Farrell et al. 2014). In recent years, the innovation of compact electronic tags and pop-up satellite transmitters (PSATs) has led to a profusion of depth and temperature distribution data of many pelagic species relative to these features with the exception of dolphinfish. Theisen and Baldwin (2012) used PSATs to document the depth and temperature distribution of wahoo (*Acanthocybium solandri*) to depths >200 m and in

Communicated by D. Righton.

**Electronic supplementary material** The online version of this article (doi:10.1007/s00227-014-2464-0) contains supplementary material, which is available to authorized users.

W. Merten (✉) · R. Appeldoorn  
Department of Marine Sciences, University of Puerto Rico  
Mayagüez, PO Box 9000, Mayagüez, PR 00681, USA  
e-mail: wessleymerten@gmail.com

W. Merten · D. Hammond  
Dolphinfish Research Program, Cooperative Science Services  
LLC, 961 Anchor Road, Charleston, SC 29412, USA

R. Rivera  
College of Business, University of Puerto Rico Mayagüez,  
PO Box 9000, Mayagüez, PR 00681, USA

water between 17.5 and 27.5 °C. White marlin (*Tetrapturus albidus*) were observed to spend the majority of their time <10 m but made frequent excursions below 100 m (Horodysky et al. 2007), while swordfish (*Xiphias gladius*) spent more time below the thermocline with maximum depths visited to >600 m (Sepulveda et al. 2010a). Many other studies have documented the habitat use of different isthophorids (Holland et al. 1990; Ortega-Garcia et al. 2008), thunnids (Block et al. 2001; Schaefer and Fuller 2007), and elasmobranchs (Weng et al. 2007; Howey-Jordan et al. 2013) deepening the knowledge base of species-specific vertical depth use in the open ocean. Understanding such movements for dolphinfish is important for describing behavioral relationships between species to develop a stronger understanding of predator–prey relationships necessary to better understand the pelagic ecosystem (Sepulveda et al. 2010b), and for both fishing and management interests for resource acquisition, bycatch prevention, and species conservation (Poisson et al. 2010).

The factors affecting the vertical position within the water column may be related over the short term to the species-specific biological responses to abiotic factors such as diel changes in light (Gleiss et al. 2013), temperature with depth (Klimley et al. 2002), or to biotic factors such as movements of prey (Gleiss et al. 2013), or differences in gender (W Merten unpublished data). Over the long term, vertical distribution may be influenced by changes in geographic location, time of year, or the seasonal position of the thermocline (Kitagawa et al. 2007; Furukawa et al. 2014). While predicting vertical position is of obvious benefit to guide fishing activities, for example to set commercial longline hook depth to target or eliminate species catch or bycatch (NMFS 2008; Poisson et al. 2010), respectively, understanding the underlying processes will be important to management, for example to predict biological responses to climate change, i.e., expansion of oxygen minimum zones (Prince et al. 2010) or changes in ocean circulation (Hurrell and Van Loon 1997). Furthermore, these data can be used to assess abundance from fishery dependent (e.g., commercial logbook catch per unit effort) or independent surveys (e.g., ship-based active hydrophone transects) (Lynch et al. 2012).

A study done on the short-term movement ecology (<48 h) of dolphinfish in the northern East China Sea found that dolphinfish remained in the upper layers of the thermocline above 20 °C, maximum depths ranged from 50.1 to 95.1 m, and a positive relationship exists between maximum diving depths and diving patterns in response to seasonal changes in the location of the thermocline (Furukawa et al. 2011, 2014). Other studies on dolphinfish have been limited to short duration investigations of site fidelity and behavior relative to drifting and stationary

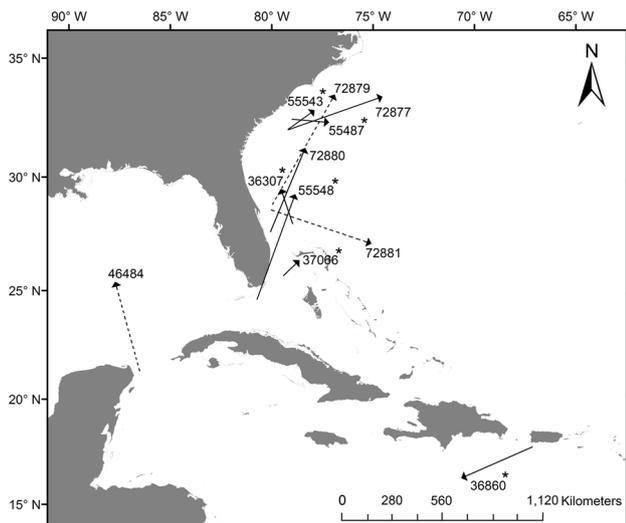
fish aggregating devices (FADs). Taguet et al. (2007) tagged dolphinfish with coded transmitters and monitored their site fidelity, habitat use, and movements relative to drifting FADs in the Indian Ocean and found that dolphinfish remained with objects on the open ocean for as much as 15.26 days and spent the majority of their time within the top 35 m of the surface. Girard et al. (2007) observed the ability of dolphinfish caught near stationary FADs to return back to the FAD when displaced up to 1,600 m away and showed variable vertical distributions, with some dolphinfish closer to the surface more often than others during the first 29 min after being released. While these data begin to describe the short-term vertical movements, residency, site fidelity, and homing abilities of dolphinfish, they do not depict the temporal periodicity and overall vertical movement strategy over longer periods of time for dolphinfish.

In this study, we investigated the vertical movements of adult male dolphinfish in the western central Atlantic as inferred from the use of high-rate single-point PSATs. The main objectives of this study were to investigate what biotic and abiotic factors may influence the diel vertical movement preferences of adult male dolphinfish. Alternative objectives were to investigate which factors may affect diel changes in duration at depth and vertical movement patterns. To achieve this, data from six PSATs deployed on dolphinfish in different regions of the western central Atlantic were analyzed. Results were used to strategize future deployments of additional PSATs and begin to design management priorities based on the information documented.

## Methods

### Satellite telemetry data

Non-geolocating single-point PSAT data were provided by the Dolphinfish Research Program from 2005 to 2011. Eleven dolphinfish (10 males, 1 female;  $110.75 \pm 7.26$  cm) were tagged and released in four different areas in the western central Atlantic and Caribbean Sea: three off South Carolina, six off Florida, one off Isla Mujeres, Mexico, and one off La Parguera, Puerto Rico (Fig. 1). All fish were tagged with Microwave Telemetry Inc., pop-up satellite archival transmitters [PSAT PTT-100 standard rate (length/diameter/antenna length/weight; 166 mm/41 mm/171 mm/65–68 g); PSAT high-rate and high-rate x-tag models (120 mm/32 mm/185 mm/40 g)]. Pop-up locations were provided by Argos using a least squares analysis algorithm. Attachment of the devices to all dolphinfish followed methods used by Merten et al. (2014).



**Fig. 1** Horizontal straight-line dolphinfish displacements from single-point PSATs varied between deployment locations around the western central Atlantic and Caribbean Sea. The ID numbers with asterisks represent the six adult male dolphinfish with high-resolution monitoring periods >3 days. Dashed lines indicate dolphinfish that were consumed by predators after being deployed. Dolphinfish 72877 was a female

#### Data selection

In this study, PSATs were preprogrammed to remain with dolphinfish for 30 or 180 days, recording time-specific water temperature, pressure, and light intensity at regular but different intervals based on tag type. At the end of the monitoring period, the device releases from the tether connecting it to the fish using electrolysis. Once the device releases, it floats to the surface and begins transmitting data to an Argos system satellite every 60 s on the SiV schedule, i.e., tags transmit for blocks of several hours when the likelihood of a satellite pass is greatest, rather than transmitting continuously. Here, only adult male dolphinfish with high-rate satellite archival records >3 days ( $n = 6$ ) were included in analyses of vertical diving behavior (only one female was tagged). The other archival records were excluded because (1) PTT-100 standard rate transmitters vary markedly in resolution and preset monitoring period from PTT-100 high rate and high-rate x-tags, (2) any record <3 days in duration was not long enough to allow for a discernible diving pattern to emerge, (3) some dolphinfish were consumed by predators after being deployed (46484, 72881, and 72879), and (4) female and male dolphinfish appear to exhibit differences in diving behavior. Summary statistics for all 11 dolphinfish are included in Appendix I. All statistical analyses of selected transmitters, except for the analysis of vertical movement patterns, were done using R<sup>®</sup> v3.0.1.

#### Diel depth use

Satellite archival time series data, including depth (m) and temperature (°C), were categorized according to four time periods, dawn (0300–0859), day (0900–1459), dusk (1500–2059), and night (2100–0259), to examine the diel periodicity of the vertical movements of dolphinfish. Moreover, these time periods were positioned relative to the timing of sunrise and sunset, based on Atlantic and Eastern Standard Time, during the spring and early summer months (April–July) that these transmitters were at liberty, in order to investigate crepuscular movement patterns, i.e., changes in vertical depth position relative to dawn and dusk. For general inference for all fish, time series depth data were aggregated for each fish into hourly means and analyzed using a linear mixed effects model (Pinheiro and Bates 2009) assigning a random effects term per fish and taking into consideration temporal dependence. Exploratory analysis revealed that the distribution of dive depths is skewed and time dependent. Hence, we take the natural logarithm of depths and incorporate an autoregressive correlation structure of order 1 (Chatfield 2009) to fit the model. Specifically for fish  $i = 1, \dots, n$ , time of day  $j = 1, \dots, n_j$  and time  $t = 1, \dots, T_i$ , we fit

$$Y_{i,j,t} = \beta_0 + \alpha_j + \beta_2 Y_{i,j,t-1} + f_i + (\alpha f)_{ij} + \varepsilon_{i,j,t}$$

where  $Y_{i,t}$  is the natural logarithm of the depth of the  $i$ th fish at hour  $t$ ,  $\alpha_j$  is the effect of the  $j$ th TOD on the response variable,  $Y_{i,t-1}$  adjusts for the temporal dependence on depth measurements,  $f_i$  is random term that adjusts the intercept per fish,  $(\alpha f)_{ij}$  handles interaction between TOD and fish, and  $\varepsilon_{i,t}$  are independent error terms. We assume  $f_i \sim N(0, \sigma_f^2)$ ,  $(\alpha f)_{ij} \sim N(0, \sigma_{\alpha f}^2)$ ,  $\varepsilon_{i,t} \sim N(0, \sigma^2)$ , and that all random terms are mutually independent.

#### Diel duration at depth

Daily changes in duration at depth were analyzed using survival analysis. Survival analysis, as defined by Kleinbaum and Klein (2012), is “a collection of statistical procedures for data analysis for which the outcome variable of interest is *time until an event occurs*.” Using the recurrent timing of dives and surface intervals, an extended Cox proportional hazards frailty model was fit to predict, by time of day, the probability a dolphinfish would remain at depth before returning to the surface to begin another dive (Kleinbaum and Klein 2012). The frailty component was modeled using a gamma distribution (Kleinbaum and Klein 2012), and recurrent dives and surface intervals used in this analysis were derived from the following criteria: (1) dives were defined as any departure from the surface (0 m) and consecutive depth fixes >0 m for any given amount of time; (2) surface intervals were defined as any consecutive depth fixes through time equal to 0 m.

## Diel vertical movement patterns

Vertical movement patterns were analyzed using a cursory visual examination of time series depth records (Horodysky et al. 2007). The analysis revealed four different movement patterns that were classified into dive types based on the appearance of time series recorded observations. Dive patterns confined to the surface layer (0–9.9 m) were defined as line-shaped dives. The line-shaped dive type was deduced from the notion of dolphinfish using their line-of-sight to guide surface movement activity relative to prey or for navigation. A v-shaped dive represented an abrupt descent to depth followed by an abrupt ascent back to the surface of 10 m or more in consecutive depth fixes. A u-shaped dive was defined as an abrupt descent to depth followed by a continuous amount of time within a few meters of that depth before ascending back to the surface. Lastly, a w-shaped dive depicts a seesaw-shaped motion with two or more directional changes in the water column from deep to shallow depths, and vice-versa, until the dive ends when a surface interval was initiated. Based on these criteria, each dive was assigned a dive type and pooled by time of day for all fish and analyzed using a chi-square analysis.

## Results

All satellite transmitter release and end point locations were widely distributed around the western central Atlantic, Caribbean Sea, and Gulf of Mexico (Fig. 1). Of the six adult male dolphinfish analyzed here, the maximum tracking duration (the time the PSAT remained attached to the dolphinfish) was 30.24 day ( $13.89 \pm 10.38$  days,  $N = 6$ ) (mean  $\pm$  SE,

$N = \#$ ) (Table 1). These archival records covering 83.37 days were acquired over a six-year period from 2005 until 2011. Average depth use from all depth fixes ( $N = 23,166$ ) of these dolphinfish was 8.53 m; maximum diving depths ranged from 74.0 to 255.5 m. The mode for depth use  $>10$  m for each adult male dolphinfish ranged from 10.8 to 44.4 m. In the following analyses, all statistical inference was based on a 5 % significance level.

## Diel depth use

A linear mixed effects model was fit to account for the correlation of within fish depth measurements. Not properly modeling depth measurements per fish may hinder inference on the impact of time of day (Pinheiro and Bates 2009). After selection for tag type and monitoring period duration (Table 1), the analysis showed that after adjusting for random effects and temporal dependence in time of day fish interaction, there were statistical differences in depth by time of day (Fig. 2). Specifically, it was found that difference in depth was statistically significant when comparing dawn (mean: 7.55 m) and day (4.76 m) to night (14.88 m) (linear mixed effects model,  $P < 0.001$ ). The intercept and interaction terms of the mixed effects model had standard deviations of 0.26 and 0.13, respectively. Hence, for any given time of day, adult male dolphinfish will have individual intercepts that are 0.26 higher or lower than the group average 68 % of the time; furthermore, individually, the time of day estimated coefficient will vary by 0.13 higher or lower than the group average estimate 68 % of the time. A multiple comparison analysis based on Tukey's method (Bretz et al. 2011) confirmed significant differences in depth use by time of day (Table 2).

**Table 1** Adult male dolphinfish with high-resolution pop-up satellite archival transmitter data records  $>3$  days in duration arranged from north to south in the western central Atlantic

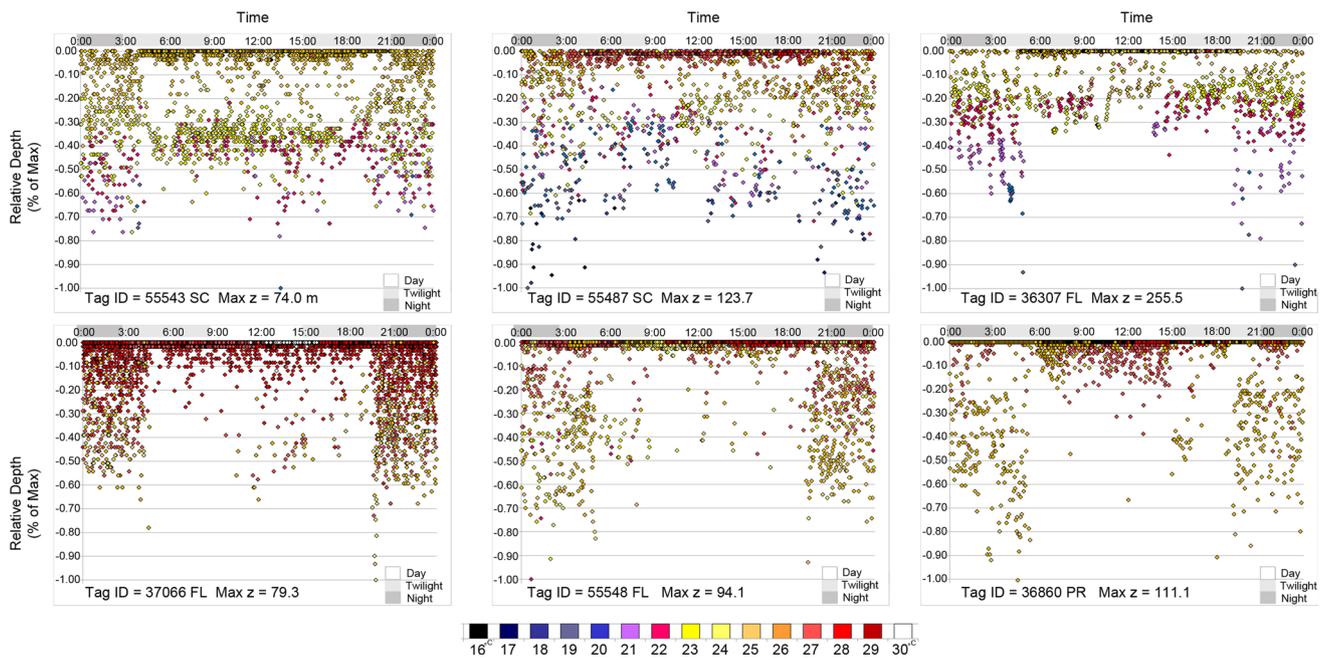
Tag (#)	Tagging date	Fork length (cm) <sup>a</sup>	Pop-up date	Monitoring period (days) <sup>b</sup>	Tag type <sup>c</sup>	Depth fixes (#)	Dives (#)	Maximum depth (m)	Average temp (°C)	Temp range (°C) <sup>d</sup>
55543	6.4.2005	107.0	6.13.2005	8.88	PTT-100	2482	156	74.0	25.05°	19–26°
55487	6.21.2006	105.0	6.27.2006	5.89	PTT-100	1907	124	123.7	25.49°	16–28°
36307	5.7.2010	97.5	5.11.2010	4.96	HI X	1498	104	255.5	24.65°	19–28°
55548	5.10.2006	112.5	5.20.2006	10.08	PTT-100	3092	266	94.1	26.86°	22–28°
37066	6.9.2006	120.0	7.2.2006	23.32	PTT-100	6321	657	79.3	28.44°	24–30°
36860	4.2.2011	108.8	5.2.2011	30.24	HI X	7866	562	111.1	27.15°	25–30°
Total				83.37		23,166	1,869			

<sup>a</sup> Estimated fork length

<sup>b</sup> Days monitoring dolphinfish

<sup>c</sup> PTT-100 and HI X: pop-up high-rate archival satellite transmitter with 30 days preset monitoring period

<sup>d</sup> Rounded down to the nearest whole number



**Fig. 2** Distribution of depth fixes based on relative depth (actual depth divided by maximum depth obtained for each dolphinfish) by time of day are positioned from north to south (clockwise from *top-left*) for adult male dolphinfish with high-resolution monitoring peri-

ods >3 days from South Carolina, Florida, and Puerto Rico. Dawn and dusk (*light gray*) were designated as twilight, where night (*dark gray*) and day (*white*) stand alone

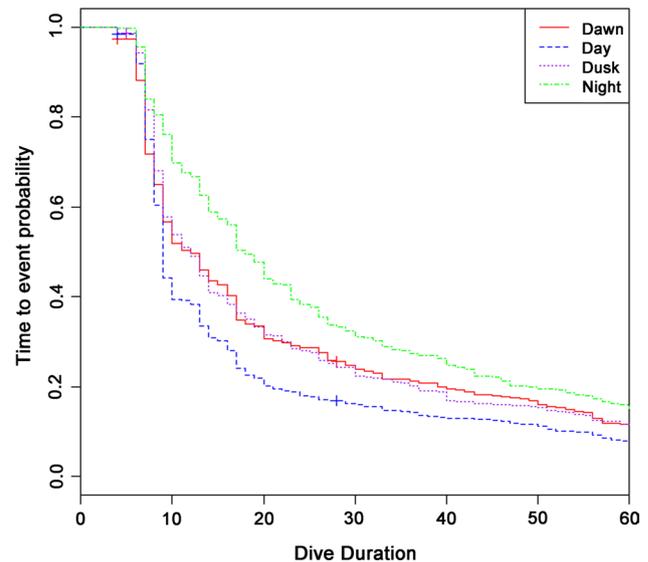
**Table 2** Multiple comparisons of average logarithm of depth based on the mixed effects model using Tukey's correction of depth use by time of day for all adult male dolphinfish with monitoring periods greater than 3 days

Time of day comparison	Estimate	Standard error	Z value	P value
b—a	-0.006096	0.092236	-0.066	1.0000
c—a	0.227632	0.092036	2.473	0.0803
d—a	0.404626	0.092672	4.366	<b><u>7.59e-05</u></b>
c—b	0.233729	0.091921	2.543	0.0660
d—b	0.410722	0.093960	4.371	<b><u>7.41e-05</u></b>
d—c	0.176993	0.093720	1.889	0.3537

Significance is indicated by bolded and underlined  $P < 0.05$ . **a** Dawn; **b** day; **c** dusk; **d** night

Diel duration at depth

There were significant differences in duration at depth per dive by time of day for adult male dolphinfish (extended Cox proportional hazard frailty model;  $P < 0.001$ ). The hazard ratio for the effect of maximum depth per dive indicated that frailty was highly significant ( $P < 0.001$ ). In particular, for any given dive duration, the probability that the fish would remain at depth was higher during night than during day (Fig. 3). In addition, the frequency of long (>60 min) deep dives (>30 m) was greatest during night (42 %



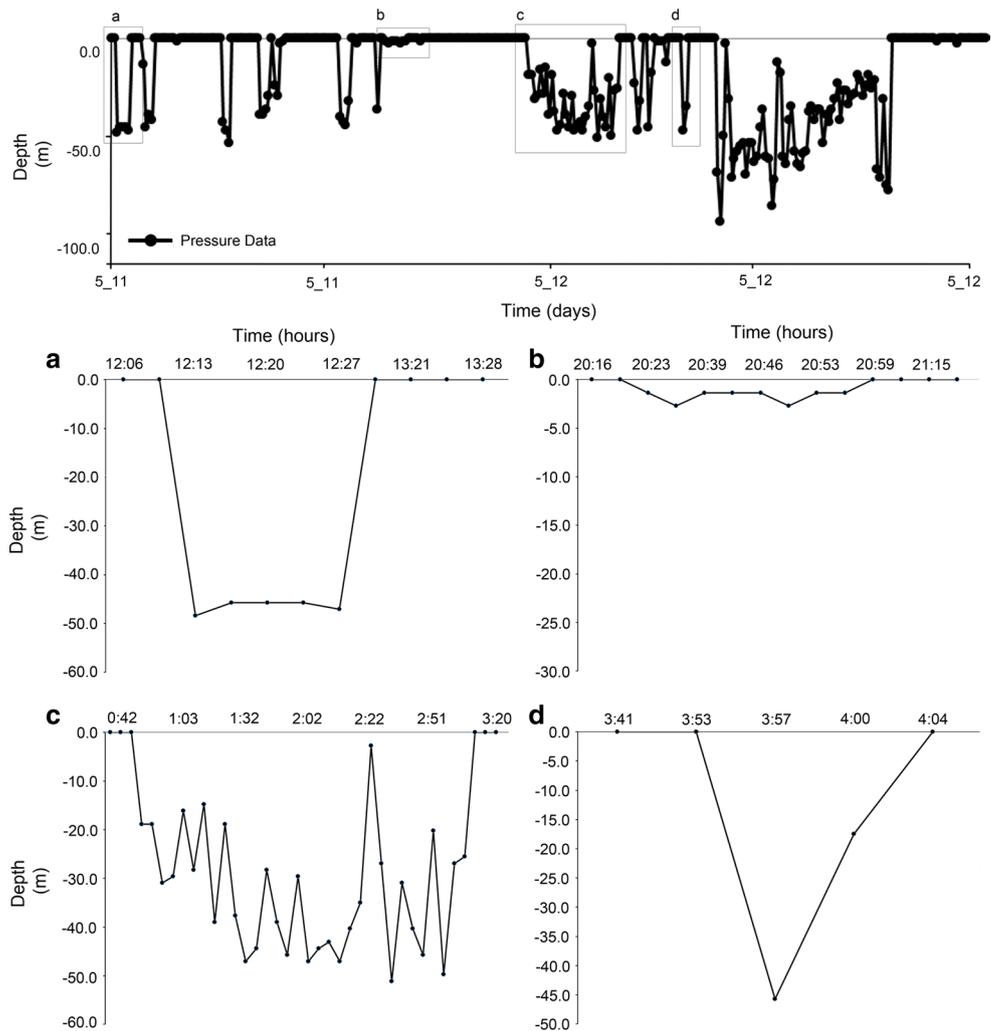
**Fig. 3** Time to event probabilities (at-depth to surface) for dives ranging in duration from 0 to 60 min by time of day estimated using the Kaplan–Meier method

$n = 192$ ) when compared to dawn (16 %  $n = 70$ ), day (9 %  $n = 47$ ), and dusk (23 %  $n = 111$ ). Maximum depth per dive was significantly greater during night (29.3 m) than during dawn (14.2 m), day (10.2 m), or dusk (19.0 m) (extended cox proportional hazard model;  $P < 0.05$ ). Based

**Table 3** Percentage of temperature readings from pop-up satellite archival transmitters attached to dolphinfish expressed as differences from maximum temperature at the surface and minimum temperature recorded in succeeding dives

Tag (#)	$\Delta T$ (°C)									
	-1	-2	-3	-4	-5	-6	-7	-8	-9	-10
55543	48.70	57.79	74.68	87.66	97.40	98.70	100.00			
55548	83.08	89.47	92.43	95.11	98.50	100.00				
37066	71.03	82.90	94.76	99.08	100.00					
55487	52.42	64.52	70.16	71.77	73.39	80.65	84.68	91.13	98.39	100.00
36307	36.54	50.00	64.42	81.73	90.38	97.12	98.08	100.00		
36860	61.26	96.22	99.46	100.00						

**Fig. 4** One day of pressure data taken from dolphinfish 55548 provides an example of how vertical movement patterns were categorized. **a** u-shaped dive; **b** line-shaped dive; **c** w-shaped dive; **d** v-shaped dive



on absolute temperature recorded during the dives, all fish remained within 10 °C of the maximum temperature recorded per monitoring period while at liberty (Table 3).

Diel vertical movement patterns

Vertical movement patterns (Fig. 4) varied significantly per dive type ( $N = 1,869$ ) by time of day (dawn;  $N = 453$ ; day;

$N = 479$ ; dusk;  $N = 480$ ; night;  $N = 457$ )(Chi square test,  $P < 0.001$ ) (Table 4). For all dolphinfish, the number of line-shaped dives was the least during the night and greatest during day. During night, w-shaped dives were greatest for each dolphinfish. Additionally, the combination of u- and w-shaped dives was greatest during night, while the combination of line and v-shaped dives were greatest during dawn, day, and dusk. For the majority of dolphinfish,

**Table 4** Chi square comparisons reveal significant differences in dive type by time of day for all adult male dolphinfish with high-resolution monitoring periods >3 days

Dive type by time of day			
Dawn	V (n = 35)	U (n = 56)	W (n = 49)
Line (n = 313)	<b><u>0.000</u></b>	<b><u>0.000</u></b>	<b><u>0.000</u></b>
V (n = 35)	–	0.028	0.127
U (n = 56)		–	0.495
W (n = 49)			–
Day	V (n = 17)	U (n = 73)	W (n = 26)
Line (n = 363)	<b><u>0.000</u></b>	<b><u>0.000</u></b>	<b><u>0.000</u></b>
V (n = 17)	–	<b><u>0.000</u></b>	0.170
U (n = 73)		–	<b><u>0.000</u></b>
W (n = 26)			–
Dusk	V (n = 37)	U (n = 98)	W (n = 59)
Line (n = 286)	<b><u>0.000</u></b>	<b><u>0.000</u></b>	<b><u>0.000</u></b>
V (n = 37)	–	<b><u>0.000</u></b>	0.025
U (n = 98)		–	0.002
W (n = 59)			–
Night	V (n = 96)	U (n = 114)	W (n = 113)
Line (n = 134)	0.012	0.204	0.181
V (n = 96)	–	0.214	0.240
U (n = 114)		–	0.947
W (n = 113)			–

Bold and underlined numbers indicate significant difference ( $P < 0.001$ )

the number of lines dives were significantly greater during dawn, day, and dusk than all other dive types (v-, u-, and w-shaped). Lastly, the amount of line dives progressed from least during night to greatest during day, the opposite for u- and w-shaped dives.

## Discussion

This study reports for the first time long-term comprehensive vertical movement activity of adult male dolphinfish observed through the use of PSATs. Overall, dolphinfish were observed more frequently in shallow depths but did make frequent dives to depths below 30 m and infrequently deeper than 200 m. The shallow diving behavior may be attributed to prey location (Oxenford and Hunte 1999), orientation with surface objects such as flotsam or *Sargassum* during migration (Hemphill 2005; Taquet et al. 2007), or in effort to minimize metabolic energy loss by remaining in isothermic conditions above the thermocline (Furukawa et al. 2011, 2014). Generally, when not in the top of the surface layer (0–1.3 m), dolphinfish most often occupied depths within the surface (1.3–9.9 m) and subsurface layer (10–29.9 m), then progressively less at deeper depths in

the mixed surface layer beginning from 30 to 59.9 m, to 60–89.9 m, and lastly >90 m (Appendix I). Based on depth use, duration at depth, and vertical movement patterns, dolphinfish partake in ritualized shifts in behavior from shallow depths during the day to deep depths at night. These data, however, are only representative of large adult male dolphinfish and may not be representative of the vertical movement strategy of younger dolphinfish or females.

Biotic factors that drive vertical movement preferences of dolphinfish

### Prey location

Dolphinfish analyzed in this study exhibited diel vertical depth use. The diel pattern in depth distribution is similar to those observed in studies of striped marlin (Holts and Bedford 1990) and sailfish (Chiang et al. 2011) where fish occupied shallow depths during day and deep depths at night. This cannot, however, be considered a general distribution pattern for large pelagic predators because blue sharks, blue marlin, and broadbill swordfish have been observed diving deeper during day than during night (Carey et al. 1990; Holland et al. 1990; Block et al. 1992a).

Dolphinfish, like other pelagic species, most likely respond to diel changes in prey location which influences their location in the water column on a daily basis. In a study monitoring the vertical movements of whale sharks, Gleiss et al. (2013) found that the sharks changed their vertical movement activity and depth location in anticipation of the formation of aggregated patches of prey items such as zooplankton at sunset. Studies on other large planktivores, such as basking sharks (Sims et al. 2005), and piscivores, such as probeagle (Saunders et al. 2011), big-eye thresher (Weng and Block 2004), and great white sharks (Weng et al. 2007), have documented diel vertical movements with the most likely explanation being that these predators are pursuing vertically migrating prey to optimize foraging efficiency. Vertically tracking prey to optimize foraging efficiency while minimizing energy consumption has been suggested as a preferred feeding strategy for many pelagic fish species (Furukawa et al. 2011, 2014; Gleiss et al. 2013).

At night, dolphinfish dove deeper for longer durations (Table 2; Fig. 3), presumably foraging. Specifically, for each dive duration, the probability that the fish would take longer to return to the surface was higher at night than all other time periods. The longer dive times at night could be representative of dolphinfish using more time to search for and exploit aggregated prey (Horodysky et al. 2007). Studies conducted in the Indian Ocean, central Pacific Ocean, Mediterranean Sea, and eastern Caribbean Sea all concluded that dolphinfish feed at night as well as during the day (Rothschild 1964; Shcherbachev 1973; Massutí et al. 1998; Oxenford and Hunte 1999). Massutí et al. (1998) observed that dolphinfish stomachs sampled at sunrise contained mesopelagic prey items such as *Eledone moschata*, *Argyropelecus hemigymnus*, *Chauliodus sloani*, and *Notolepis rissoi*. However, across all studies, the greater proportion of epipelagic prey items (e.g., Exocoetidae, Clupeidae, Carangidae, Scombridae) indicates that dolphinfish forage mainly in surface and subsurface layers (0–30 m) but can make excursions to depths to feed opportunistically on mesopelagic fishes and invertebrates that undergo diel vertical migration from depth during the day to more shallow waters at night.

Diel differences in vertical movement patterns likely reflect changes in dolphinfish feeding dynamics. The v-, u-, and w-shaped dive types (Fig. 4) were more frequently observed during night than dawn, day, or dusk (Table 4) indicating that dolphinfish vertical movement patterns vary by time of day. It is hypothesized that different shaped dives are indicative of different responses to daily changes in prey location in the water column (Horodysky et al. 2007; Gleiss et al. 2011a). V- and w-shaped dives involve rapid directional changes presumably increasing prey encounter

rates without extensively increasing travel distance (Horodysky et al. 2007); alternatively, these directional changes could also be a response to avoiding predators. U- and line-shaped dives are likely a response to targeting prey that is aggregating for extended periods of time (Horodysky et al. 2007). Line dives were the greatest during day supporting a surface-oriented foraging pattern targeting epipelagic prey; a deeper foraging pattern targeting mesopelagic prey for extended periods of time is reflected in a greater amount of u-shaped dives at night. Other factors that could influence diving behavior are moving vertically, as opposed to horizontally, to obtain olfactory or visual cues for navigation, or for prey silhouetting (Davies et al. 1999).

### Surface objects

A bimodal vertical depth distribution (Fig. 2) was observed indicating that when dolphinfish are not at the surface they are at intermediate depths (between 10 and 40 % of maximum observed depth) during the day. It is not known whether this behavior is related to orientation below surface floating objects (e.g., *Sargassum* or flotsam) to aid in predation, predator avoidance, or for navigation purposes. Studies done on the movements and homing ability of dolphinfish relative to stationary and drifting fish aggregating devices (FADs) have observed depth distributions within 35 m of the surface, dives as deep as 144 m, varied excursion frequencies, and homing abilities all of which seem to indicate that dolphinfish may adjust their swimming depths with respect to potential orientation cues based on light and sound (Girard et al. 2007; Dagorn et al. 2007; Taquet et al. 2007), with the former dominating near the surface and the latter dominating away from surface interference. Dempster and Kingsford (2003) suggest that dolphinfish may use sounds produced by the FAD itself, or by fish associated with it, to aid in navigation and association with surface structures. Furthermore, dolphinfish have been observed to occupy floating objects for up to 2 weeks and display the ability to navigate back to an object after being displaced 1.6 km away (Girard et al. 2007; Dagorn et al. 2007) which suggests their migration is influenced by the movements of floating objects (Merten et al. 2014a, b). Results from the present study confirm that dolphinfish are strongly tied to the surface during daylight hours, when surface objects would be most visible. Analysis of gut contents in various studies have found that the majority of the daytime diet of dolphinfish consists of teleost fishes that presumably would be consumed near the surface under floating mats of *Sargassum* or any other structure that promotes the aggregation of juvenile fish and invertebrates (Rothschild 1964; Massutí et al. 1998; Oxenford and Hunte 1999). Indeed, both *Sargassum* and teleost prey items have been found

together in the stomachs of sampled dolphinfish (Manooch et al. 1983). Thus, these studies suggest that the voracious feeding activity of dolphinfish and the importance of structure-associated prey in their diet may drive the observed pattern of daylight surface activity.

Alternatively, daytime association with surface objects is likely to aid in predator avoidance. Large toothed whales, such as false killer whales, have been documented to pursue dolphinfish (Merten et al. in press), and gut content analyses of large marlin have revealed dolphinfish as a prey source (Pimenta et al. 2001). While surface objects are for obvious reasons an area to increase foraging efficiency for dolphinfish, they like the prey they are pursuing and are most likely also associating with surface objects to reduce predation risk through schooling (Dagorn et al. 1995). The dynamics of dolphinfish schooling behavior relative to surface objects is poorly documented (Taquet et al. 2007); however, surface objects seem to serve as an exchange site for individuals moving between schools (Taquet et al. 2007) and affords a location for increased group size that reduces the overall probability of individual predation risk (Gooding and Magnuson 1967). Studies have shown that smaller dolphinfish associate with surface objects more than larger fish (Farrell et al. 2014) supporting the meeting point hypothesis that surface objects serve as a refuge for smaller fish more susceptible to predation (Fréon and Dagorn 2000). Here, a bimodal vertical daytime depth distribution could be indicative of larger fish possibly orienting below surface objects to aid in both foraging activities and to reduce predation risk by remaining below the well-lit surface waters in the shadow cast by large surface objects. The precise vertical movements, however, relative to surface objects (FADs and *Sargassum*) need to be further investigated to provide a more thorough understanding of the role they play in influencing dolphinfish vertical depth use across all size classes.

Abiotic factors that influence vertical movement preferences of dolphinfish

#### *Temperature and oxygen*

Dives below the thermocline were evident, but marked movements relative to the thermocline were indiscernible. The majority of the dolphinfish, however, occupied temperatures within 8 °C of the maximum temperature observed at the surface (Table 3; Fig. 2); dolphinfish 55487 experienced temperature changes >8 °C from the surface (minimum 16.8 °C) during only 8 % of its dives ( $n = 124$ ). These observations are consistent with another study done on dolphinfish where all fish remained on average in temperatures greater >19 °C (Furukawa et al. 2011). Furukawa

et al. (2011) concluded that dolphinfish avoid transcending the thermocline to conserve energy and focus their feeding strategies on epipelagic prey in the isothermic surface layer. Studies of blue and striped marlin, and sailfish, were similar in that vertical movements were limited by a ~8 °C relative change in water temperature with depth (Pepperell and Davis 1999; Chiang et al. 2011) suggesting their physiological thermal constraints may be similar as with dolphinfish. In contrast, the broadbill swordfish (*Xiphias gladius*) has been observed to dive as deep as 673 m, with differences from sea surface temperature ranging from 8.7° to 17.6 °C colder (Sepulveda et al. 2010a, 2010b); however, this species has pronounced physiological features such as brain-eye energy-producing muscles which may facilitate deeper diving behavior by maintaining higher organ temperatures in the head (Carey 1982). Therefore, while dolphinfish may be eurythermal (e.g., range 16.80–30.09 °C), their overall vertical movement strategy will be limited by depths whose temperatures minimize energy consumption due to lack of physiological adaptations, i.e., heat producing organs or more efficient gill morphology, needed to forage efficiently in colder temperatures (Wegner et al. 2010).

Seasonal changes in thermocline location and formation of oxygen minimum zones may influence the maximum vertical habitat use of dolphinfish (Stramma et al. 2012; Prince et al. 2010; Furukawa et al. 2014). In the East China Sea, dolphinfish were observed to extend their vertical depth range as the thermocline depth increased (Furukawa et al. 2014), and in the eastern tropical Atlantic, sailfish and blue marlin were found to limit their vertical movements relative to the depth, location, and extent of oxygen minimum zones leading to habitat compression in the upper portion of the surface mixed layer (Prince et al. 2010); similar conditions and responses have been observed in the eastern tropical Pacific for the same species (Prince and Goodyear 2006). In the western Atlantic where dissolved oxygen is not limited at increasing depths, fish can extend their vertical depth range beyond those observed in the eastern tropical Pacific or Atlantic (Prince et al. 2010). In this study, for example, multiple dolphinfish repeatedly visited depths >200 m in the Gulf Stream, similar to results for sailfish and blue marlin from the same area (Prince et al. 2010). In the Caribbean Sea, where the thermal vertical stratification and distribution of biogeochemical properties of the mixed surface layer is more pronounced (Corredor and Morell 2001; Jury 2011), the vertical extent of a single dolphinfish was 111 m and never >4 °C of maximum recorded surface temperatures. These observations support geographic variations in vertical depth use of dolphinfish but require more extensive intra and inter-oceanic comparisons to draw more concrete conclusions about regional differences in both space and time.

## Light

Generally, for dolphinfish, the greatest percentage of time spent at the surface was during dawn, day, and dusk, and least during the night, though the significance of these time of day effects varied by fish. The greatest overall difference in depth use was observed between day and night, and dawn and night time periods; dawn and dusk appear to be transition periods when fish return to the surface after a night of deeper depth use, or begin deeper depth use, respectively. Daily changes in dive patterns are also reflected in depth usage; at night, depth usage is normally distributed, a stark contrast to the bimodal periodicity observed during day (Fig. 2). The change in daily depth distribution is likely a result of dolphinfish exhibiting different activity patterns or behaviors that are apparently linked with prey location, as discussed earlier, that have been shown to respond to daily changes in light (Gleiss et al. 2011b).

Indeterminate factors that influence vertical movement preferences of dolphinfish

## Lunar phase and gender

Lunar phase and gender may be other factors affecting the vertical movements of dolphinfish. Captains who target large pelagic fish believe that lunar phase positively influences landing rates (Poisson et al. 2010). In a recent re-analysis of the literature, however, Ortega-Garcia et al. (2008) found little support that catch per unit effort is influenced by phase of the moon for striped marlin, but some studies have shown that the activity level of certain pelagic fishes is correlated with the lunar cycle (Horodysky et al. 2007; Poisson et al. 2010). Horodysky et al. (2007), when examining white marlin found an increased amount of higher complexity dives during nights with brighter moon phases. In this study, only two dolphinfish had monitoring periods long enough (30.24 and 23.32 days) to make adequate comparisons between moon phase and diving behavior parameters such as dive duration, surface interval duration, maximum depth per dive, and vertical movement pattern. Yet, when comparing diving behavior trends among the two, they were generally opposite, i.e., duration at depth and vertical movement patterns were greater during the full moon for dolphinfish 37066, but were greater during new moon for dolphinfish 36860. However, both dolphinfish did partake in longer surface intervals during the new moon versus full moon phase, which translated into less dives throughout all time periods. Only with the acquisition of more high-resolution monitoring periods (>21 days) can the influence of lunar phase on vertical movements be further addressed.

Female dolphinfish may exhibit different vertical movements than males. Only one female has been tagged to date, but the results are intriguing. For example, the female (107.5 cm FL) tagged and released off South Carolina revealed a diving behavior opposite than that of adult males, with deepest depths (maximum 247 m) visited during dawn, day, and dusk, rather than night. Gender-specific differences in vertical movements of male and female dolphinfish may be related to size (Oxenford and Hunte 1999), feeding preferences, or increased tendency to associate with surface objects (Farrell et al. 2014).

## Management and future research priorities

General inference into the vertical movements of adult male dolphinfish is provided with this work. Indeed, the results provide significant insight into their vertical movements, but more records are needed to correlate temperature constraints, lunar phase, and vertical movement patterns between different regions (i.e., South Atlantic Bight vs Caribbean Sea) or oceans (western central Atlantic versus eastern tropical Pacific). It does appear, however, that the vertical extent of dolphinfish habitat use varies between the South Atlantic Bight and the Caribbean Sea presumably due to differences in prevailing oceanographic conditions between the two regions (Bane and Dewar 1988; Corredor and Morell 2001; Jury 2011). As a result, to prevent dolphinfish by-catch during commercial longline operations, gear should be set at depths based on the prevailing oceanographic conditions (i.e., location of the thermocline) while taking into account regional differences in the vertical extent of dolphinfish. To make these recommendations on a broader scale, more high-rate PSATs (programmed for 30 day monitoring periods) should be deployed among and between regions and ocean basins to conduct valid regional comparisons. In addition, only PSAT records from large adult male dolphinfish were examined in this study, and these are therefore un-representative of younger and smaller dolphinfish (<8–10 months) and females. While there exist some data on movements of small dolphinfish relative to drifting and stationary FADs (Dagorn et al. 2007; Girard et al. 2007; Taquet et al. 2007) and the thermocline (Furukawa et al. 2011), young of the year dolphinfish (<90 cm) need to be tagged with high-rate PSATs (suggested transmitter size; <12 cm; suggested transmitter weight; <40 g) if comparisons of habitat use between size classes are to be determined. In addition, large adult females need to be sampled in order to assess sex-specific differences in vertical movement strategies by time of day. Deploying high-rate satellite transmitters on both male and female dolphinfish of differing sizes will benefit both fishing and managerial interests through determining gender-specific vertical movement differences relative to depth,

biogeochemical properties such as dissolved oxygen, and can lead to enhanced landings or to prevent dolphinfish by-catch during commercial operations. These data and the insight they provide will enhance our understanding of dolphinfish habitat use in the open ocean and when used accordingly can lead to improved fishery management and future dolphinfish conservation.

**Acknowledgments** This research was supported by funding through the Marine Resources Division of the South Carolina Department of Natural Resources, the Cooperative Science Services, LLC., Dolphinfish Research Program and the U.S. Fish and Wildlife and Puerto Rico Department of Natural and Environmental Resources F-66.1 grant awarded to the Department of Marine Sciences at the University of Puerto Rico Mayaguez. We would like two anonymous reviewers for providing valuable suggestions during their reviews of earlier versions of this manuscript. We would like to thank all of the recreational, charter, and commercial fisherman, and all of the businesses, organizations, and individuals for their financial support making this study possible. Your dedication to the advancement of our understanding of dolphinfish is gratefully acknowledged.

## References

- Bane JM Jr, Dewar WK (1988) Gulf stream bimodality and variability downstream of the Charleston Bump. *J Geophys Res* 93:6695–6710. doi:[10.1029/JC093iC06p06695](https://doi.org/10.1029/JC093iC06p06695)
- Block BA, Booth DT, Carey FG (1992) Depth and temperature of the blue marlin, *Makaira nigricans*, observed by acoustic telemetry. *Mar Biol* 114:175–183
- Block BA, Dewar H, Blackwell SB, Williams TD, Prince ED, Farwell CJ, Boustany A, Teo SLH, Seitz A, Walli A, Fudge D (2001) Migratory movements, depth preferences, and thermal biology of Atlantic bluefin tuna. *Science* 293:1310–1314
- Bretz F, Hothorn T, Westfall P (2011) Multiple comparisons using R. Chapman and Hall/CRC, Boca Raton. ISBN 13-978-1-4200-1090-9
- Carey FG (1982) A brain heater in swordfish. *Science* 216:1327–1329
- Carey FG, Scharold JV, Kalmijn AJ (1990) Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar Biol* 106:329–342
- Chatfield C (2009) The analysis of time series: an introduction. Texts in statistical science, Sixth edition edn. Chapman and Hall/CRC, Boca Raton. ISBN 1-58488-317-0
- Chiang W-C, Musyl MK, Sun C-L, Chen S-Y, Chen W-Y, Liu D-C, Su W-C, Yeh S-Z, Fu S-C, Huang T-L (2011) Vertical and horizontal movements of sailfin shark (*Istiophorus platypterus*) near Taiwan determined using pop-up satellite tags. *J Exp Mar Biol Ecol* 397:129–135. doi:[10.1016/j.jembe.2010.11.018](https://doi.org/10.1016/j.jembe.2010.11.018)
- Corredor J, Morell M (2001) Seasonal variation of physical and biogeochemical features in the eastern Caribbean surface water. *J Geophys Res* 106:4517–4525
- Dagorn L, Stretta JM, Petit M (1995) Tropical tuna associated with floating objects: a simulation study of the meeting point hypothesis. *C J Fish Aqua Sci* 56:984–993
- Dagorn L, Pincock D, Girard C, Holland K, Taquet M, Sancho G, Itano D, Aumeeruddy R (2007) Satellite-linked acoustic receivers to observe behavior of fish in remote areas. *Aquat Living Resour* 20:307–312. doi:[10.1051/alr:2008001](https://doi.org/10.1051/alr:2008001)
- Davies RW, Fuiman LA, Williams TM, Collier SO, Hagely WP, Kanatous SB, Kohin S, Horning M (1999) Hunting behavior of a marine mammal beneath the Antarctic fast ice. *Science* 283:993–996
- Dempster T, Kingsford MJ (2003) Homing of pelagic fish to fish aggregating devices (FADs): an investigation of the role of sensory cues. *Mar Ecol Prog Ser* 258:213–222
- Farrell ER, Boustany AM, Halpin PN, Hammond DL (2014) Dolphinfish (*Coryphaena hippurus*) distribution in relation to biophysical ocean conditions in the northwest Atlantic. *Fish Res* 151:177–190. doi:[10.1016/j.fisheries.2013.11.014](https://doi.org/10.1016/j.fisheries.2013.11.014)
- Fréon P, Dagorn L (2000) Review of fish associative behaviour: toward a generalisation of the meeting point hypothesis. *Rev Fish Biol Fisheries* 10:183–207
- Furukawa S, Kawabe R, Ohshimo S, Fujioka K, Nishihara GN, Tsuda Y, Aoshima T, Kanehara H, Nakata H (2011) Vertical movements of dolphinfish *Coryphaena hippurus* as recorded by acceleration data-loggers in the northern East China Sea. *Environ Biol Fish* 92:89–99
- Furukawa S, Tsuda Y, Nishihara GN, Fujioka K, Ohshimo S, Tomoe S, Nakatsuka N, Kimura H, Aoshima T, Kanehara H, Kitagawa T, Chiang WC, Nakata H, Kawabe R (2014) Vertical movements of Pacific bluefin tuna (*Thunnus orientalis*) and dolphinfish (*Coryphaena hippurus*) relative to the thermocline in the northern East China Sea. *Fish Res* 14:86–91. doi:[10.1016/j.fishres.2013.09.004](https://doi.org/10.1016/j.fishres.2013.09.004)
- Girard C, Dagorn L, Taquet M, Aumeeruddy R, Peignon C, Benhamou S (2007) Homing abilities of dolphinfish (*Coryphaena hippurus*) displaced from fish aggregating devices (FADs) determined using ultrasonic telemetry. *Aquat Living Resour* 20:313–321. doi:[10.1051/alr:2008005](https://doi.org/10.1051/alr:2008005)
- Gleiss AC, Norman B, Wilson RP (2011a) Moved by that sinking feeling: variable diving geometry underlies movement strategies in whale sharks. *Func Eco* 25:595–607. doi:[10.1111/j.1365-2435.2010.01801.x](https://doi.org/10.1111/j.1365-2435.2010.01801.x)
- Gleiss AC, Jorgensen SJ, Liebsch N, Sala JE, Norman B, Hays GC, Quintana F, Grundy E, Campagna C, Trites AW, Block BA, Wilson RP (2011b) Convergent evolution in locomotory patterns of flying and swimming animals. *Nat Comm* 2:352–358. doi:[10.1038/ncomms1350](https://doi.org/10.1038/ncomms1350)
- Gleiss AC, Wright S, Liebsch N, Wilson RP, Norman B (2013) Contrasting diel patterns in vertical movement and locomotor activity of whale sharks at Ningaloo Reef. *Mar Biol*. Doi:[10.1007/s00227-013-2288-3](https://doi.org/10.1007/s00227-013-2288-3)
- Gooding RM, Magnuson JJ (1967) Ecological significance of a drifting object to pelagic fishes. *Pac Sci* 21:486–497
- Hemphill H (2005) Conservation on the high seas—drift algae habitat as an open ocean cornerstone. *Parks* 15:48–56
- Holland K, Brill R, Chang RKC (1990) Horizontal and vertical movements of Pacific blue marlin captured and released using sport-fishing gear. *Fish Bull US* 88:397–402
- Holts D, Bedford D (1990) Activity patterns of striped marlin in the southern California Bight. In: Stroud RH (ed) Planning the future of billfishes. National Coalition Marine Conservation, Savannah, pp 81–93
- Horodysky AZ, Kerstetter DW, Latour RJ, Graves JE (2007) 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. *Fish Oceanogr* 16:240–256. doi:[10.1111/j.1365-2419.2006.00419.x](https://doi.org/10.1111/j.1365-2419.2006.00419.x)
- Howey-Jordan LA, Brooks EJ, Abercrombie DL, Jordan LKB, Brooks A, Williams S, Gospodarczyk E, Chapman DD (2013) Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the Oceanic Whitetip (*Carcharhinus longimanus*) in the western north Atlantic. *PLoS ONE* 8:1–12. doi:[10.1371/journal.pone.0056588](https://doi.org/10.1371/journal.pone.0056588)
- Hurrell JW, Van Loon H (1997) Decadal variations in climate associated with the north Atlantic oscillation. *Clim Change* 36:301–326
- Jury MR (2011) Environmental influences on Caribbean fish catch. *Int J Oceano* 1-11 doi:[10.1155/2011/174729](https://doi.org/10.1155/2011/174729)

- Kitagawa T, Boustany AM, Farwell CJ, Williams TD, Castleton MR, Block BA (2007) Horizontal and vertical movements of juvenile bluefin tuna (*Thunnus orientalis*) in relation to seasons and oceanographic conditions in the eastern Pacific Ocean. *Fish Oceanogr* 16:409–421. doi:10.1111/j.1365-2419.2007.00441.x
- Kleinbaum DG, Klein M (2012) *Survival analysis: A Self-Learning Text*. Statistics for Biology and Health, Third Edition, Springer Science and Business Media doi:10.1007/978-1-4419-6646-9\_1
- Klimley AP, Beavers SC, Curtis TH, Jorgensen SJ (2002) Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. *Env Biol Fish* 63:117–135
- Lynch PD, Shertzer KW, Latour RJ (2012) Performance of methods used to estimate indices of abundance for highly migratory species. *Fish Res* 125–126:27–39. doi:10.1016/j.fishres.2012.02.005
- Mahon R (1999) Dolphinfish fisheries in the Caribbean region. *Sci Mar* 63:411–420
- Manooch CSI, Mason DL, Nelson RS (1983) Food and gastrointestinal parasites of dolphin, *Coryphaena hippurus*, collected along the southeastern and gulf coasts of the United States. *US Dep Commer NOAA Tech Memo NMFS- SEFC* 124:1–36
- Massuti E, Deudero S, Sánchez P, Morales-Nin B (1998) Diet and feeding of dolphin (*Coryphaena hippurus*) in western Mediterranean waters. *Bull Mar Sci* 63:329–341
- Merten W, Rodriguez G (in press) First stranding and sighting of the false killer whale (*Pseudorca crassidens*) off Puerto Rico. *Carib J Sci*
- Merten W, Appeldoorn R, Hammond D (2014a) Movements of dolphinfish (*Coryphaena hippurus*) along the US east coast as determined through mark and recapture data. *Fish Res* 151:114–121. doi:10.1016/j.fishres.2013.10.021
- Merten W, Appeldoorn R, Hammond D (2014b) Spatial differentiation of dolphinfish (*Coryphaena hippurus*) movements relative to the Bahamian archipelago. *Bull Mar Sci* 90. doi:10.5343/bms.2013.1078
- National Marine Fisheries Service (2008) Report of the U.S. longline bycatch reduction assessment and planning workshop. U.S. Dep Commerce, NOAA Tech Memo NMFS-OPR-41, pp 1–50
- Ortega-Garcia S, Ponce-Diaz G, O'Hara R, Merila J (2008) The relative importance of lunar phase and environmental conditions on striped marlin (*Tetrapturus audax*) catches in sport fishing. *Fish Res* 93:190–194. doi:10.1016/j.fishres.2008.04.005
- Oxenford H, Hunte W (1983) Age and growth of dolphin, *Coryphaena hippurus*, as determined by growth rings in otoliths. *Fish Bull* 84:1–7
- Oxenford H, Hunte W (1986) Preliminary investigation of the stock structure of the dolphin, *Coryphaena hippurus*, in the western central Atlantic. *Fish Bull* 84:451–460
- Oxenford H, Hunte W (1999) Feeding habits of the dolphinfish (*Coryphaena hippurus*) in the eastern Caribbean. *Sci Mar* 63:303–315
- Oxenford HA, Murray PA, Luckhurst BE (2003) The biology of wahoo (*Acanthocybium solandri*) in the western central Atlantic. *Gulf Caribb Res* 15:33–49
- Pepperell JG, Davis TLO (1999) Post-release behavior of black marlin, *Makaira indica*, caught off the Great Barrier Reef with sport-fishing gear. *Mar Biol* 135:369–380
- Pimenta EG, Marques FR, Lima GS, Amorim AF (2001) Marlin project: tag-and-release, biometrics and stomach content of billfish in Cabo Frio City, Rio de Janeiro, Brazil. *Collect Vol Sci Pap ICCAT* 53:371–375
- Pinheiro JC, Bates DM (2009) *Mixed-effects models in S and S-PLUS*. Statistics and Computing, Springer
- Poisson F, Gaertner JC, Taquet M, Durbec JP, Bigelow K (2010) Effects of lunar cycle and fishing operations on longline-caught pelagic fish: fishing performance, capture time, and survival of fish. *Fish Bull* 108:268–281
- Prince ED, Goodyear CP (2006) Hypoxia-based habitat compression of tropical pelagic fishes. *Fish Oceanogr* 15:451–464
- Prince ED, Lou J, Goodyear CP, Hoolihan JP, Snodgrass D, Orbesen ES, Serafy JE, Ortiz M, Schirripa MJ (2010) Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes. *Fish Oceanogr* 19:448–462. doi:10.1111/j.1365-2419.2010.00556.x
- Rothschild BJ (1964) Observations on dolphins (*Coryphaena* spp.) in the central Pacific Ocean. *Copeia* 1964:445–447
- Saunders RA, Royer F, Clarke MW (2011) Winter migration and diving behavior of porbeagle shark, *Lamna nasus*, in the north-east Atlantic. *ICES J Mar Sci* 68:166–174. doi:10.1093/icesjms/fsq145
- Schaefer KM, Fuller DW (2007) Vertical movement patterns of skipjack tuna (*Katsuwonus pelamis*) in the eastern equatorial Pacific Ocean, as revealed with archival tags. *Fish Bull* 105:379–389
- Sepulveda CA, Aalbers SA, Ortega-Garcia S, Wegner NC, Bernal D (2010a) Depth distribution and temperature preferences of wahoo (*Acanthocybium solandri*) off Baja California Sur, Mexico. *Mar Biol* 158:917–926. doi:10.1007/s00227-010-1618-y
- Sepulveda CA, Knight A, Nasby-Lucas N, Domeier ML (2010b) Fine-scale movements of the swordfish *Xiphias gladius* in the Southern California Bight. *Fish Oceanogr* 19:279–289. doi:10.1111/j.1365-2419.2010.00543.x
- Shcherbachev YN (1973) The biology and distribution of the dolphins (Pisces, Coryphaenidae). *J Ichthyol* 13:182–191
- Sims DW, Southall EJ, Tarling GA, Metcalfe JD (2005) Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *J Anim Ecol* 74:755–761
- Stramma L, Prince ED, Schmidtko S, Luo J, Hoolihan JP, Visbeck M, Wallace DWR, Brandt P, Körtzinger A (2012) Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes. *Nat Clim Change* 2:33–37. doi:10.1038/NCLIMATE1304
- Taquet M, Dagorn L, Gaertner JC, Girard C, Aumerruddy R, Sancho G, Itano D (2007) Behavior of dolphinfish (*Coryphaena hippurus*) around drifting FADs as observed from automated acoustic receivers. *Aquat Living Resour* 20:323–330. doi:10.1051/alr:2008008
- Theisen TC, Baldwin JD (2012) Movements and depth/temperature distribution of the ectothermic Scombrid, *Acanthocybium solandri* (wahoo), in the western north Atlantic. *Mar Biol* 159:2249–2258. doi:10.1007/s00227-012-2010-x
- Wegner NC, Sepulveda CA, Bull KB, Graham JB (2010) Gill morphometrics in relation to gas transfer and ram ventilation in high-energy demand teleosts: scombrids and billfishes. *J Morph* 271:36–49
- Weng KC, Block BA (2004) Diel vertical migration of the bigeye thresher shark (*Alopias superciliosus*), a species possessing orbital retina mirabilia. *Fish Bull* 102:221–229
- Weng KC, Boustany AM, Pyle P, Anderson SC, Brown A, Block BA (2007) Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Mar Biol* 152:877–894. doi:10.1007/s00227-007-0739-4