



Movement behaviour of released wild and farm-raised dolphinfish *Coryphaena hippurus* tracked by pop-up satellite archival tags

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Abstract

To gauge the effectiveness of supplementing native populations of dolphinfish *Coryphaena hippurus*, we compared farm-raised and wild fish in terms of their horizontal and vertical movement patterns, habitat preferences and thermal niche using pop-up satellite archival tags (PSATs) deployed in two disparate locations: the sub-tropical southeastern coast of Taiwan (wild, $n = 4$), and temperate Kagoshima Bay, Japan (farm-raised, $n = 3$). Tagged fish were tracked for periods of 7–40 days, reached depths > 100 m, and experienced temperatures of 15–30 °C in Taiwan, and 20–23 °C in Kagoshima Bay. Fish tagged in Taiwan made primarily northward movements during early summer but changed to a southward course in early winter. In Kagoshima Bay, tagged fish undertook southward excursions along the coast and movements were confined to the bay. Dolphinfish spent > 50% of their time near the surface and made more extensive vertical movements during the night than during the day; vertical movements were largely confined to the mixed layer. Depth distributions appeared to be limited by a $\Delta 6$ °C change in temperature relative to sea surface temperature (i.e., > 90% of movements were within 6 °C of the warmest water available).

Keywords Diel · Habitat · Kalman filter · Most probable tracks · Thermal niche

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Introduction

Shifts in the horizontal and vertical movement patterns of fish can change their vulnerability to fishing gear and thus complicate population assessments based on catch-per-unit-effort (CPUE) data (Brill and Lutcavage 2001). Understanding the movement behavior of fish is necessary for regional stock assessments and to inform fisheries management. Before the advent of electronic tags, it was difficult to observe and appreciate the diverse array of movement behaviors, habitat preferences and migratory patterns exhibited by wild fish populations (Block et al. 1998, 2001). The advent of pop-up satellite archival tags (PSATs) has provided researchers with an independent method to track and archive movements and behavioral characteristics of pelagic species such as bluefin tuna (Wilson et al. 2005), wahoo (Theisen and Baldwin 2012), white marlin (Horodysky et al. 2007), and swordfish (Sepulveda et al. 2010).

Dolphinfish *Coryphaena hippurus* is an epipelagic species with a circumtropical distribution that mainly inhabits the uniform surface mixed layer in tropical and subtropical environments (Palko et al. 1982). The species is often found in neritic habitats around structures and debris and is known to migrate along the coastlines of many countries (Kojima 1964; Palko et al. 1982). The stock structure of dolphinfish is enigmatic and difficult to clarify, and there are many uncertainties about their temporal-spatial habitat characteristics and movement patterns at different life stages. Dolphinfish support important recreational and commercial fisheries and researchers in the Western Central Atlantic used temporal-spatial changes in CPUE data to estimate horizontal movement patterns (Pérez et al. 1992). Furthermore, in support of informing stock assessments, Merten et al. (2014a, b, c) also used PSATs to study the vertical movements of dolphinfish in the Western Central Atlantic, which indicated primary residence in the surface mixed layer and some diel trends (e.g., deeper excursions at nighttime than daytime). In the East China Sea, Furukawa et al. (2011, 2014) studied short-term behavior (< 48 h) of dolphinfish and reported a positive correlation between maximum diving depth and depth of the top of the thermocline, thus confirming the general observations of other researchers in different locations. In comparison to similar epipelagic species, dolphinfish exhibit a much shallower vertical distribution than striped marlin (*Kajikia audax*) (Brill et al. 1993) and sailfish *Istiophorus platypterus* (Chiang et al. 2011, 2013).

Though recent genetic research using mtDNA markers suggested possible sub-division between populations of dolphinfish from Japan and Taiwan (Lu et al. 2019), for management purposes; the populations—both served

by the Kuroshio Current—are considered to comprise the same stock (Chang et al. 2013). As identified in the Fishery Improvement Plan, information on the horizontal and vertical movement behaviors of the dolphinfish was considered inadequate for informing stock assessments in Taiwan (SFPWeb: <https://www.sustainablefish.org/News/SFP-Urges-Stock-Wide-Assessments-of-Pacific-Mahi-in-First-Sustainability-Overview-Report> “Accessed 8 Jun 2018”). Moreover, to combat local stock depletion, in addition to catch regulations and habitat protection, supplementing wild populations with aquaculture recruits from local broodstock remains a viable option. However, for this to be a practical strategy, farm-raised recruits need to exhibit similar behaviors to wild populations. Given the large body of literature on dolphinfish aquaculture and farming (Balon 2004; Lorenzen et al. 2012), supplementing wild populations with farm-raised local broodstock offers a cost-effective method to maintain genetic diversity and introduce new recruits to the fishery (Hedrick et al. 2000; Hilderbrand 2002). Survival rates of wild and farm-raised fish, however, have been reported to be different (Aarestrup et al. 2014; Johnsson et al. 2014). To gauge if supplementing wild populations is feasible, the cooperative study presented here was undertaken to understand movement behaviors of wild and farm-raised dolphinfish.

Materials and methods

PSAT models X-Tag and High Rate X-Tag (Microwave Telemetry, Columbia, MD) were programmed to release 240 and 30 days after deployment, respectively. The tags were programmed with a suite of fail-safe options for reporting in cases of mortality or premature release (Musyl et al. 2011a). At the surface, PSATs transmit data to Argos; the X-Tag had variable memory capability and acquired temperature and pressure data every 15 min for the first 4 months, at 30-min intervals at 4–8 months, and at hourly intervals > 8 months. The HR X-Tag had a higher memory capacity and acquired temperature and pressure data every 4 min for a period of 30 days. Specifications for temperature and pressure data points in the tags ranged from −4 to 40 °C and from 0 to 1296 m, respectively (resolution 0.16–0.23 °C, 0.34–5.4 m).

PSATs were deployed on presumably healthy specimens > 80-cm fork length captured from longline boats fishing out of Taitung, Taiwan (wild) and dip-netted from an aquaculture facility in Kagoshima Bay, Japan (farm-raised). The tagged dolphinfish in Japan were caught from the East China Sea and farm-raised in Kagoshima Bay for 4 months. Farm-raised dolphinfish were fed on small fish and the ambient water of the aquaculture facility was taken from Kagoshima Bay. Prior to tag insertion, a wet towel was placed over the eyes of the fish to calm them and a

hose carrying seawater (without brass connections) was put into their mouths for ventilation. The PSAT was fitted with a nylon umbrella tag head and fluorocarbon tether and inserted approximately 6 cm into the dorsal musculature with a 35-cm tagging pole. The tag heads and tethers were disinfected with alcohol and bacitracin-neomycin ointment was applied before tagging to prevent wound ulceration and infection. Location of tag deployments were recorded using the Global Positioning System.

After popping-up, the tags relayed archived data via Argos including pressure (depth), temperature and geolocation data (note: HR X-Tags do not provide raw geolocation estimates). Raw light-based geolocation points were calculated and provided by the manufacturer (Musyl et al. 2011a). We filtered these raw geolocations by removing impossible latitudes (<0 or >59) and longitudes (<115 or >150). Next, we applied an unscented Kalman filter [augmented with sea surface temperature (SST)] to calculate most probable tracks (MPTs) from the raw geolocations (Lam et al. 2008).

Linear displacements from tagging to pop-up locations were determined using the great-circle distance and pop-up locations were estimated by Doppler shift using Argos messages with location classes of one or higher.

Archived time series for pressure (depth) and temperature were categorized into daytime and nighttime periods by calculating times of local sunrise and sunset time (<http://aa.usno.navy.mil/>). To further explore daytime and nighttime differences, we used one-sample Kolmogorov–Smirnov tests to compare distributions of ambient temperature and depth data to that of a normal distribution; all were non-normally distributed. As a result, we used non-parametric two-sample Kolmogorov–Smirnov and Mann–Whitney *W*-tests to compare differences in medians between daytime and nighttime data for depth and temperature distributions (Zar 2010). The α -level for multiple pairwise comparisons was adjusted with the Bonferroni correction to compensate for multiple tests of the same hypothesis. Thermal habitat distributions were expressed as differences (Δ SST) from average daily SST estimates from the tags (Brill et al. 1993; Musyl et al. 2011b; Nielsen et al. 2006). Time-at-depth and time-at-temperature data were aggregated into 5-m and 1-°C bins, respectively, and expressed as a fraction of the total time calculated for each fish. Vertical characteristics of the water column of the deployment site in southeastern Taiwan were obtained from conductivity-temperature-depth (CTD) casts (Ocean Seven 304 CTD Logger). In Kagoshima Bay, vertical characteristics of the water column were obtained from the Asia–Pacific Data–Research Center (APDRC) (<http://apdrc.soest.hawaii.edu/>).

In addition to the statistical analyses described above, vertical movement patterns of the time series of depth records were also analyzed using visual methods according to Horodysky et al. (2007). The visual analysis was partitioned into

three distinct dive types: dive patterns confined to the surface layer (0–10 m) were defined as surface movement (surface movement type was deduced from dolphinfish using their line-of-sight to guide surface movement activity relative to prey movements or for navigation purposes (Davis et al. 1999); a the “w-complex” dive pattern depicted a seesaw motion with two or more directional changes in the water column from deep to shallow depths, and vice versa, until the dive ended with prolonged residency at the surface; lastly, “v-shaped” dive patterns represented an abrupt descent followed by an abrupt ascent back to the surface of 10 m or more in consecutive depth fixes. Based on these criteria, each dive was assigned a dive type and data were pooled for the four astronomical periods (dawn, daytime, dusk, nighttime) for all fish.

Results

Deployment duration and data retrieval

From 2014 to 2017, seven PSATs were deployed on dolphinfish ranging from 81- to 113-cm fork length; four wild dolphinfish were tagged on the coast in southeastern Taiwan and three farm-raised dolphinfish were tagged in Kagoshima Bay, Japan (Fig. 1). Tag retention periods were variable and four PSATs detached prematurely within 20 days while two in Kagoshima Bay stayed attached for 30 and 40 days, respectively (Table 1). Data return rates in the PSATs was calculated following methods given in Musyl et al. (2011a). The amount of data downloaded is compared to the maximum possible expected amount when all data points (i.e., depth, temperature, geolocation) are received for the time at liberty given the rate of data acquisition. Data return rates ranged from 1 to 91% and averaged 32% for depth, temperature and geolocation (Table 1). Since data return from tag no. (#) 163105 was 1%, this tag was excluded from the analysis of vertical movement data.

Horizontal movements

Linear displacements from deployment to pop-up locations in Taiwan (164–296 km, average 22 km) and Kagoshima Bay (28–46 km, average 0.9 km) translated into daily displacement rates of 9.3–42 km day⁻¹ (average 1.6 km day⁻¹) and 0.9–2.3 km day⁻¹ (0.07 km day⁻¹), respectively. Pronounced directed movements were observed in the MPTs. The movements of farm-raised dolphinfish in Kagoshima Bay, Japan were confined to the bay, with #163106 making a directed southerly excursion (Fig. 1). According to the MPTs, after being tagged in April, wild dolphinfish #132762 traveled 237 km in 15 days (15.8 km day⁻¹) from Orchid Island (Lanyu)

Fig. 1 Deployment and pop-up locations for dolphinfish carrying pop-up satellite archival tags (PSATs). Filled circles are deployment location, dashed lines straight-line movements and filled triangles pop-up locations

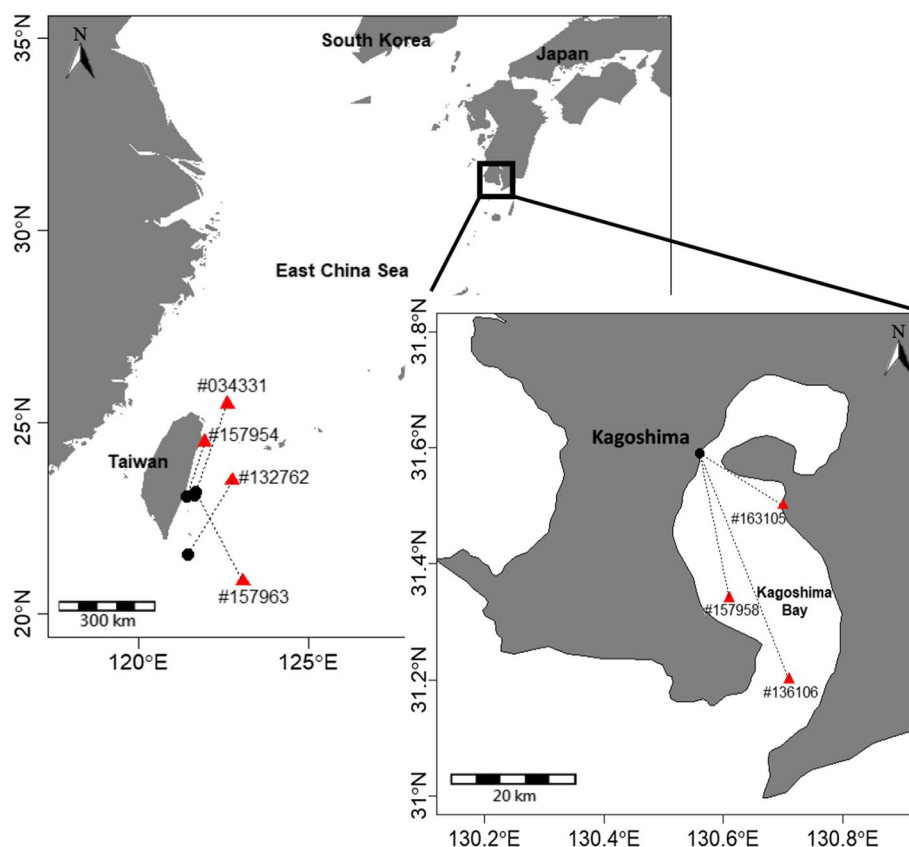


Table 1 Details for pop-up satellite archival tags (PSATs) deployed on dolphinfish

PSAT no. (#)	Sex	Fork length (cm)	Deployment date	Location	Reporting date	DAL ^a (day)	Straight-line distance ^a (km)	Data return rate ^b (%)	Tag type
132762	M	113	17 April 2014	Southeastern Taiwan	2 May 2014	15	237	26	X-tag
157954	M	102	19 May 2016	Southeastern Taiwan	27 May 2016	8	164	33	HR X-tag
157963	F	99	17 October 2016	Southeastern Taiwan	23 October 2016	7	296	91	X-tag
034331	M	106	14 July 2017	Southeastern Taiwan	12 August 2017	30	281	38	X-tag
163106	M	84	9 November 2016	Kagoshima Bay	29 November 2016	20	46	19	X-tag
157958	F	81	9 November 2016	Kagoshima Bay	9 December 2016	30	28	21	HR X-tag
163105	F	86	9 November 2016	Kagoshima Bay	19 December 2016	40	17	1	X-tag

^aDays at liberty (DAL) and straight-line distance are from deployment to pop-up location

^bData return rate represents the averages of depth, temperature and geolocation data (see text for explanation)

and moved northward to near Yonaguni, Japan (Fig. 2). Dolphinfish carrying PSAT #157963 traveled 296 km southward in 7 days (42.3 km day^{-1}) from the Chenggong coast after being tagged in October. After being tagged in July, dolphinfish #034331 traveled 281 km in 30 days

(9.4 km day^{-1}) travelling northwards along the coast of Taiwan to the East China Sea (Fig. 2).

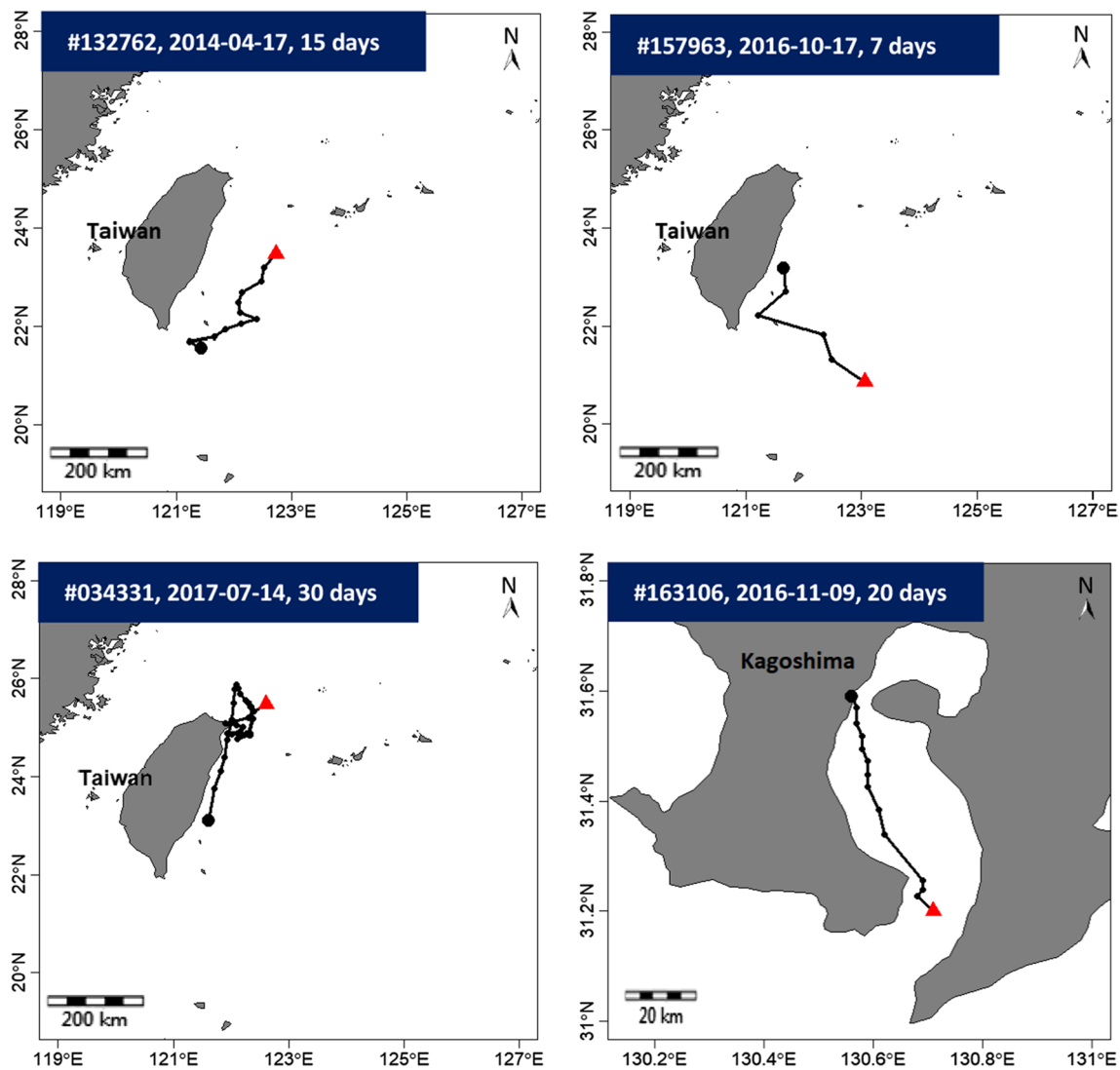


Fig. 2 Individual tracks of dolphinfish tagged in the southeastern Taiwan [nos. (#) 132762, #157963 and #034331] and Kagoshima Bay, Japan (#163106). Fish deployment positions (filled circles), points

estimated from most probable tracks from state-space Kalman filter movement model (black dots and lines) and pop-up locations (filled triangles)

Vertical behavior and vertical movement patterns

We obtained a total of 60 and 50 days of depth and temperature data, respectively, from the six PSATs in the analysis. The diel vertical distributions of wild and farm-raised fish were largely restricted to within 100 m of the surface (Fig. 3) between 18 and 30 °C (Table 2; Fig. 4). Wild and farm-raised dolphinfish exhibited strong fidelity to the sea surface (0–5 m) at daytime and nighttime. Compared to wild dolphinfish from Taiwan (daytime, 72%; nighttime, 47%), farm-raised dolphinfish stayed almost exclusively at the sea surface in Kagoshima Bay (daytime, 95%; nighttime, 93%). The main thermal preference (95% confidence intervals) for tagged dolphinfish was 26–28 °C in Taiwan and 21–22 °C in Kagoshima Bay (Fig. 4). Although conditions between

the two habitats are different, the commonality of the data suggests dolphinfish inhabit water above 20 °C.

Two-sample Kolmogorov–Smirnov and Mann–Whitney *W*-tests were significantly different between tags ($p < 0.001$) for 95% of all possible pairwise comparisons for day and night distributions of depth and temperature data, which indicates a high level of individual variability in movement patterns. No patterns emerged to explain movement differences based on origin (farm-raised and wild fish), body size or sex.

In the individual dive patterns, surface dives mainly occurred at dawn, during the day and dusk, and w-complex dives were observed during dusk and at night. The combination of v-shaped and w-complex dives was mainly observed during nighttime (Fig. 5).

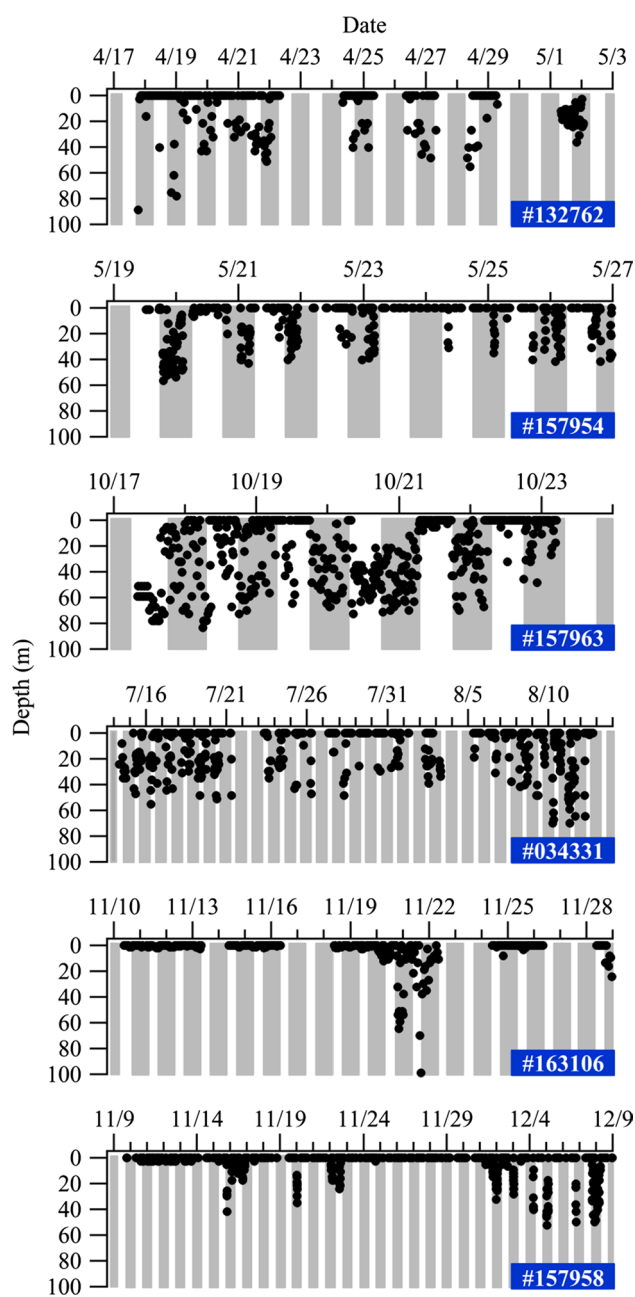


Fig. 3 Time-depth series of dolphinfish tagged in southeastern Taiwan (#132762, #157954, #157963 and #034331) and Kagoshima Bay, Japan (#163106 and #157958). Grey vertical bars indicate night-time

Mixed layer and temperature threshold

In Kagoshima Bay, temperature-depth profiles were within the mixed layer depth (MLD) and limited to water temperatures above 20 °C (Fig. 6) and the bottom of the MLD appears to be ~80 m in southeastern Taiwan. According to vertical temperature gradients, dolphinfish vertical

Table 2 Summary of the depth and temperatures obtained for PSATs deployed on dolphinfish

PSAT #	Day depth (m) min.–max. (mean ± SD)	Night depth (m) min.–max. (mean ± SD)	Day temp. (°C) min.–max. (mean ± SD)	Night temp. (°C) min.–max. (mean ± SD)
132762 (Southeastern Taiwan)	0–89 (8.1 ± 14.3)	0–78 (13.4 ± 18.2)	23.1–27.7 (26.5 ± 0.6)	23.7–27.3 (26.3 ± 0.7)
157954 (Southeastern Taiwan)	0–40 (1.7 ± 5.9)	0–57 (14.4 ± 16.6)	26.7–29.7 (28.2 ± 0.4)	25–28.6 (27.7 ± 0.6)
157963 (Southeastern Taiwan)	0–83 (20.9 ± 26)	0–73 (28.5 ± 23)	23.2–29.1 (28 ± 1.4)	23.6–29.1 (28 ± 1.3)
034331 (Southeastern Taiwan)	0–70 (9.9 ± 15.2)	0–69 (16.1 ± 16.3)	21.7–30 (27.2 ± 1.7)	21.4–30.1 (26.7 ± 1.7)
163106 (Kagoshima Bay)	0–99 (3.1 ± 9.9)	0–65 (4.7 ± 11.3)	17.9–22.7 (22 ± 0.5)	21–22.7 (22.1 ± 0.3)
157958 (Kagoshima Bay)	0–24 (0.3 ± 1.6)	0–52 (3.8 ± 9.6)	20.5–23.6 (22.1 ± 0.7)	20.5–23.2 (22.1 ± 0.7)

Minimum (*min.*), maximum (*max.*) and mean are provided with SD for depth and temperature (*temp.*) data recorded by PSATs

movements appeared to be limited by the ~25 °C isotherm (Fig. 7).

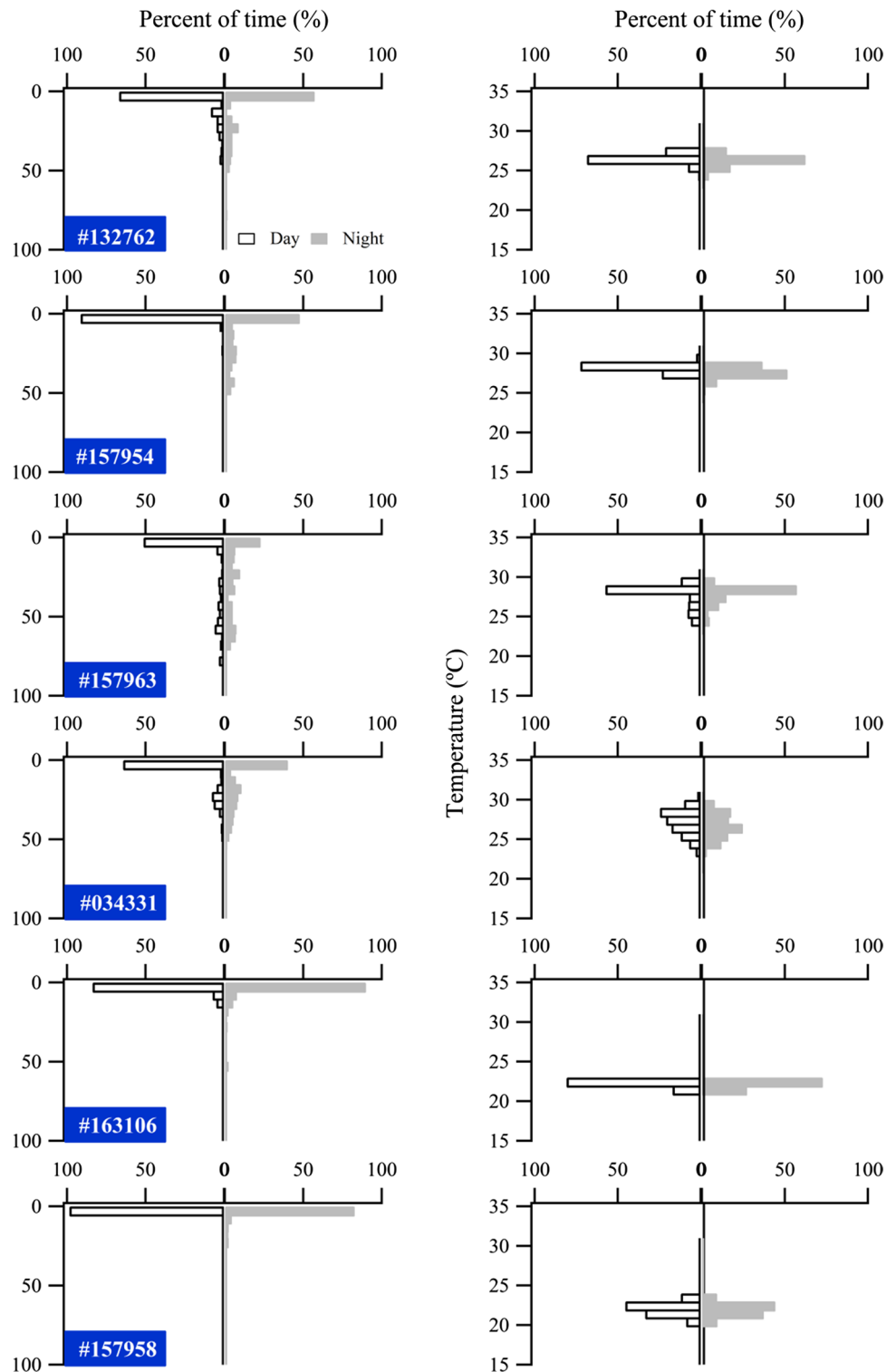
The minimum temperature, SST and maximum depth experienced by tagged dolphinfish indicate that most of their time was spent in uniform temperature of the mixed layer, above 20 °C (Fig. 8), and the Δ SST analysis showed that >90% of movements were within 6 °C of the warmest water (Table 3).

Discussion

Horizontal movements

Though separated by the Kuroshio Current, for management purposes, Pacific dolphinfish in Taiwan and Japan are considered to comprise the same stock (Chang et al. 2013). In Taiwan, dolphinfish are reported to spawn year-round off the east coast with peak activity during February and March. However, despite this activity, Taiwan is not considered a major spawning ground for the Pacific dolphinfish (Wu et al. 2001). Sampled female dolphinfish with oocytes of diameter > 1.0 mm (defined as mature eggs) have been reported from December to March and June–July in eastern Taiwan. Highest catch rates are reported for April–June and September–November, and the size mode changes seasonally, with larger fish landed in summer and smaller fish entering the fishery in winter (Chang et al. 2013). Very small (year-0) fish are present in January and again appear in June/July, which is consistent with a two-season spawning hypothesis, and results in biannual recruitment to the fishery (Chang et al. 2013). Another interpretation of the data is that the two peaks in abundance may also reflect separate spawning

Fig. 4 Percent time distribution of swimming depth and ambient temperature during daytime (*open black horizontal bars*) and nighttime (*filled horizontal grey bars*) of tagged dolphinfish. Fish were tagged in southeastern Taiwan (#132762, #157954, #157963 and #034331) and Kagoshima Bay, Japan (#163106 and #157958)



migrations. During recruitment periods, the Kuroshio Current provides ideal foraging conditions with abundant food resources that are the main components of dolphinfish diet such as flying fish, Japanese anchovy and squid (Hsieh et al. 2007; Sassa et al. 2008; Wang et al. 2008; Chang et al. 2012).

In Taiwan, the horizontal movement tracks suggested that the wild dolphinfish tagged in early summer moved in a northerly direction and that those tagged in early winter moved in a southerly direction, but tag retention times were short. In Kagoshima Bay, farm-raised dolphinfish moved southward but the tags did not remain attached to

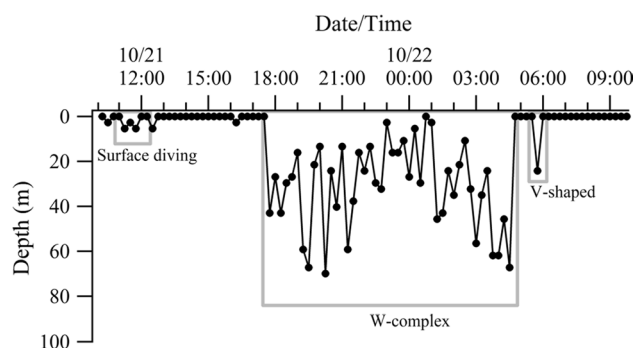


Fig. 5 Vertical movements of dolphinfish #157963 (southeastern Taiwan) were categorized into three types: surface dive, v-shaped dive, and w-complex dive. W-complex pattern occurred at night (grey shaded bar) whereas the other patterns are mostly representative of daytime activity

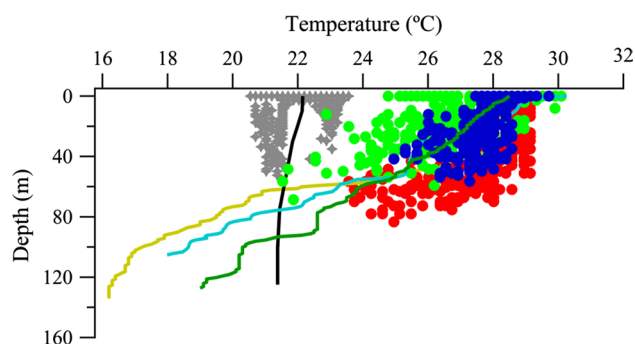


Fig. 6 Temperature-depth profiles obtained from the aggregated data from fish tagged in southeastern Taiwan [#157954, $n=757$ (blue symbols); #157963, $n=448$ (red symbols); #034331, $n=312$ (green symbols)] and fish tagged in Kagoshima Bay, Japan (gray symbols, $n=1908$). Solid colored lines represent the vertical temperature-depth profiles from conductivity-temperature-depth casts; Asia-Pacific Data Research Center (APDRC) data are given by the black line (<http://apdrc.soest.hawaii.edu/>)

the fish for prolonged periods. The SST off eastern Taiwan was ~ 26 – 28 °C during summer and 26 – 29 °C in winter and in Kagoshima Bay, ~ 20 – 23 °C. According to the analysis of catch rates by SST gradients, the highest numbers of dolphinfish occurred mostly at ~ 21 °C (Gibbs and Collette 1959; Shcherbachev 1973); $\sim 80\%$ of dolphinfish were captured at water temperatures of 25 – 28 °C by the Mexican tuna purse-seine fishery (Martínez-Rincón et al. 2009). Dolphinfish in our study were primarily found in surface waters at 27 – 29 °C, which corresponds to their distribution in the Gulf of California at 28 – 30 °C (Flores et al. 2008), and in the western central Atlantic at > 20 °C (Merten et al. 2014b). Although the tags did not stay attached for extended periods, which was needed to discern migration pathways, the vertical data indicated distinct trends. Additional tagging studies, including electronic tags and conventional plastic tags, are required to help elucidate the seasonal and inter-annual

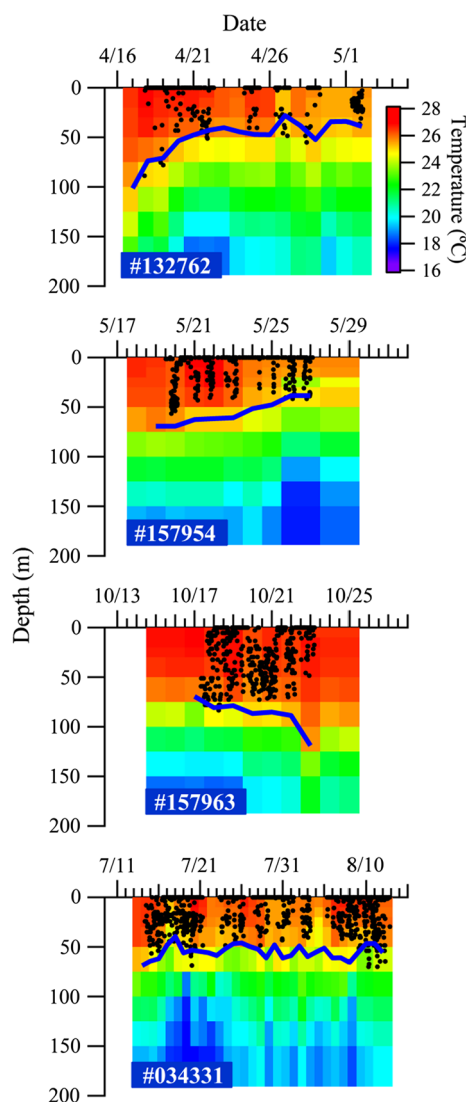


Fig. 7 Depth distribution for dolphinfish (black circles), 25 °C isotherm depth (solid blue line) and vertical water column thermal structure in southeastern Taiwan. Color scale indicates ambient water temperature

horizontal movement patterns of dolphinfish in Taiwan and Japan. Furthermore, these data are required to provide the necessary geospatial information to inform fisheries management for possible habitat protection and to refine indices of abundance.

Vertical movements

Though wild and farm-raised dolphinfish showed distinct diel vertical migration patterns (deeper excursions at night than in the day), both groups showed a preference for the upper ~ 5 m of the water column at all times of the day, which is consistent with previous studies (Furukawa et al. 2011, 2015; Merten et al. 2014a, b; Whitney et al.

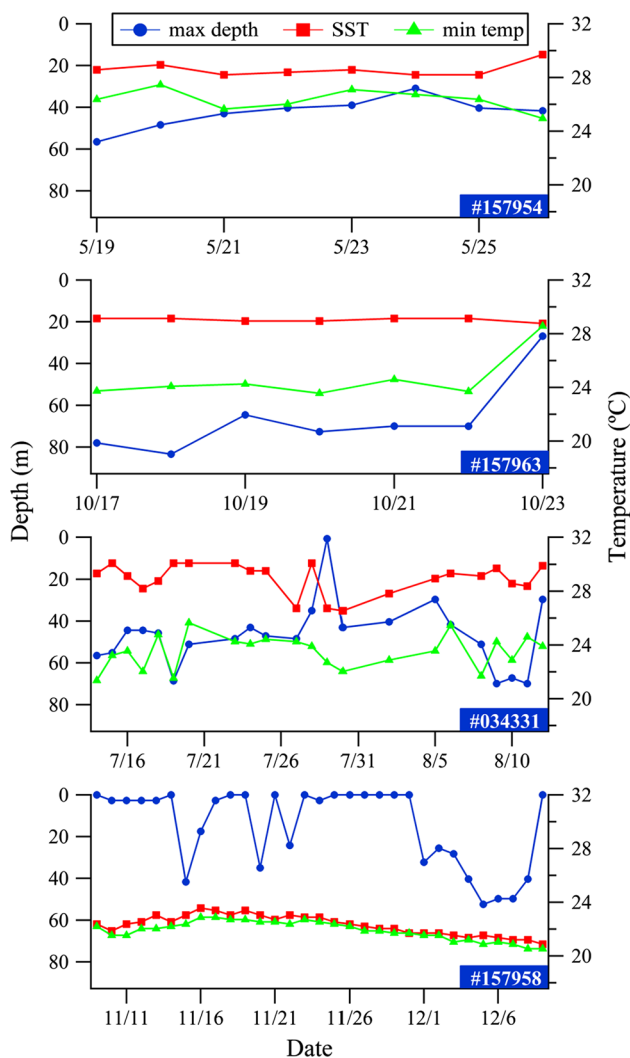


Fig. 8 Minimum (*min*) temperature (*temp*), sea surface temperature (*SST*) and maximum (*max*) depth achieved by the tracked dolphin-fish. Fish were tagged in southeastern Taiwan (#157954, #157963 and #034331) and Kagoshima Bay, Japan (#157958)

2016). Shcherbachev (1973) concluded from the presence of partially digested flying fish, myctophids, and squid that dolphinfish fed around the clock in the Indian Ocean. The present study documented dolphinfish at the surface during daylight hours. Many studies on dolphinfish have reported their daytime diet to consist mostly of teleosts (Rothschild 1964; Massutí et al. 1998; Oxenford and Hunte 1999; Olson and Galván-Magaña 2002). However, Olson and Galván-Magaña (2002) suggested that dolphinfish feed mainly at night, and many of the prey items found in their guts were

flying fish, cephalopods, and juvenile dolphinfish, wahoo, and snake mackerel. Rothschild (1964) described dolphinfish as actively feeding on flying fish and myctophids during nighttime in the central Pacific, whereas Massutí et al. (1998) found that the stomachs of almost half of the dolphinfish examined at sunrise contained mesopelagic prey such as musky octopus *Eledone moschata*, hatchetfish *Argyrops hemigymnus*, Sloane's viperfish *Chauliodus sloani*, and spotted barracudina *Notolepis rissoi*. According to the above references, dolphinfish foraging appears to encompass both daytime and nighttime periods. During the day, dolphinfish consume prey in the uniform temperature surface layer but at night have the opportunity to feed on different prey organisms of the deep sound-scattering layer during their nocturnal vertical migrations to the surface (Whitney et al. 2016). Larger male dolphinfish inhabit deeper depths than smaller females (Wu et al. 2001; Alejo-Plata et al. 2011; Zúñiga-Flores et al. 2011); however, we did not have adequate data to test these relationships. Size and sexual differences in dolphinfish, however, are of relevance for different clustering of individuals and foraging patterns (Rose and Hassler 1974).

Diel vertical movement patterns vary according to time of day and likely reflect changes in prey distribution, predator avoidance, and/or changing oceanographic conditions. Crepuscular dives are likely a response to aggregating prey organisms that are adjusting their own diel cycles based on prey availability, predator avoidance and physiological limitations (Musyl et al. 2003; Horodysky et al. 2007).

The v-shaped and w-complex dive types were more frequently observed during nighttime than during daytime or crepuscular periods, which correlates with an energetic foraging hypothesis for the exploitation of aggregated prey (Horodysky et al. 2007). Another possible hypothesis for deep dive patterns at night is an efficient travel mechanism. V-shaped dives throughout the water column, rather than continuous linear swimming near the surface, would be more energy efficient for the location of prey (Carey and Robison 1981). w-complex dives involve rapid directional changes that presumably increase the chance of prey encounters without extensively increasing linear travel distances (Thompson et al. 1991; Horodysky et al. 2007). W-complex dives could also reflect a pattern used to avoid or confuse predators by changing contrast and/or silhouettes. According to previous studies (e.g., Carey et al. 1990; Chiang et al. 2015), dolphinfish could avoid predators that spend more time at the sea surface at night by undertaking deeper and more varied w-complex dives. Other factors that could

Table 3 Cumulative percentage of temperature readings from PSATs attached to dolphinfish

PSAT #		Δ SST									
		Time	0	-1	-2	-3	-4	-5	-6	-7	-8
132762	Day	21.22	90.61	98.78	100						
(Southeastern Taiwan)	Night	9.96	80.09	93.07	99.57	100					
157954	Day	20.00	89.44	98.43	100						
(Southeastern Taiwan)	Night	20.51	82.69	92.95	99.04	100					
157963	Day	15.79	69.63	76.52	84.21	91.50	97.17	100			
(Southeastern Taiwan)	Night	11.20	64.40	76.80	89.60	94.40	98.80	100			
034331	Day	3.25	7.40	15.52	24.00	45.13	67.87	90.07	96.75	99.28	
(Southeastern Taiwan)	Night	1.61	6.22	20.97	37.56	56.22	77.88	90.32	97.69	99.53	
163106	Day	32.24	98.03	98.03	99.34	99.34	100				
(Kagoshima Bay)	Night	4.37	99.51	100							
157958	Day	34.41	100								
(Kagoshima Bay)	Night	15.33	99.89	100							

Expressed as differences of daily mean sea surface temperatures (Δ SST). SST calculated as per Nielsen et al. (2006) and is analogous to Brill et al.'s (1993) surface layer

influence vertical movement behavior and complex dives are enhanced opportunities to locate prey through olfactory plumes or visual cues (e.g., which would increase opportunities to discern prey silhouettes); it is possible that these factors may be important for navigation (Carey et al. 1990; Davies et al. 1999).

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Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

References

- Aarestrup K, Baktoft H, Koed A, Villar-Guerra DD, Thorstad EB (2014) Comparison of the riverine and early marine migration behaviour and survival of wild and hatchery-reared sea trout *Salmo trutta* smolts. *Mar Ecol Prog Ser* 496:197–206
- Alejo-Plata C, Díaz-Jaimes P, Salgado-Ugarte IH (2011) Sex ratios, size at sexual maturity, and spawning seasonality of dolphinfish (*Coryphaena hippurus*) captured in the Culf of Tehuantepec, Mexico. *Fish Res* 110(1):207–216
- Balon EK (2004) About the oldest domesticates among the fishes. *J Fish Biol* 65(Suppl. 1):1–27
- Block BA, Dewar H, Farwell C, Prince ED (1998) A new satellite technology for tracking the movements of Atlantic bluefin tuna. *Proc Natl Acad Sci USA* 95(16):9384–9889
- 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
- Brill RW, Lutcavage M (2001) Understanding environmental influences on movements and depth distributions of tunas and billfishes can significantly improve population assessments. *Am Fish Soc Sym* 25:179–198
- Brill RW, Holts DB, Chang RKC, Sullivan S, Dewar H, Carey FG (1993) Vertical and horizontal movements of striped marlin (*Tetrapturus audax*) near the Hawaiian Islands, determined by ultrasonic telemetry, with simultaneous measurement of oceanic currents. *Mar Biol* 117:567–574
- Carey FG, Robison BH (1981) Daily patterns in the activities of swordfish, *Xiphias Gladius*, observed by acoustic telemetry. *Fish Bull* 79:277–292
- Carey FG, Scharold JV, Kalmijn AJ (1990) Movements of blue sharks (*Prionace glauca*) in depth and course. *Mar Biol* 106:329–342
- Chang SK, Chang CW, Ame E (2012) Species composition and distribution of the dominant flyingfishes (Exocoetidae) associated with the Kuroshio Current, South China Sea. *Raffles Bull Zool* 60:539–550
- Chang SK, DiNardo G, Farley J, Brodziak J, Yuan ZL (2013) Possible stock structure of dolphinfish (*Coryphaena hippurus*) in Taiwan coastal waters and globally based on reviews of growth parameters. *Fish Res* 147:127–136
- Chiang WC, Musyl MK, Sun CL, Chen SY, Chen WY, Liu DC, Su WC, Yeh SZ, Fu SC, Huang TL (2011) Vertical and horizontal movements of sailfish (*Istiophorus platypterus*) near Taiwan determined using pop-up satellite tags. *J Exp Mar Biol Ecol* 397:129–135
- Chiang WC, Kawabe R, Musyl MK, Sun CL, Hung HM, Lin HC, Watanabe S, Furukawa S, Chen WY, Chen YK, Liu DC (2013) Diel oscillations in sailfish vertical movement behavior in the East China Sea. *J Mar Sci Tech* 21:267–273
- Chiang WC, Muyl MK, Sun CL, DiNardo G, Hung HM, Lin HC, Chen SC, Yeh SZ, Chen WY, Kuo CL (2015) Seasonal movements and diving behaviour of black marlin (*Istiompax indica*) in the northwestern Pacific Ocean. *Fish Res* 166:92–102
- Davis 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
- Flores MSZ, Ortega-García S, Klett-Traulsen A (2008) Interannual and seasonal variation of dolphin fish (*Coryphaena hippurus*) catch rates in the southern Gulf of California, Mexico. *Fish Res* 94:13–17
- Furukawa S, Kawabe R, Ohshimo S, Fujioka K, Nishihara GN, Tsuda Y, Aoshima T, Kanehara H (2011) Vertical movement 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* 149:86–91
- Furukawa S, Chiang WC, Watanabe S, Hung HM, Lin HC, Yeh HM, Wang SP, Tone K, Kawabe R (2015) The first record of peritoneal cavity temperature in free-swimming dolphinfish *Coryphaena hippurus* by using archival tags, on the east coast of Taiwan. *J Aquat Mar Biol* 2:1–7
- Gibbs JRH, Collette BB (1959) On the identification, distribution, and biology of the dolphin, *Coryphaena hippurus* and *C. equiselis*. *Bull Mar Sci* 9:117–152
- Hedrick PW, Hedgecock D, Hamelberg S, Croci SJ (2000) The impact of supplementation in winter-run chinook salmon on effective population size. *J Hered* 91:112–116
- Hilderbrand RH (2002) Simulating supplementation strategies for restoring and maintaining stream resident cutthroat trout populations. *N Am J Fish Manage* 22:879–887
- 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
- Hsieh HY, Lo WT, Liu DC, Hsu PH, Su WC (2007) Winter spatial distribution of fish larvae assemblages relative to the hydrography of the waters surrounding Taiwan. *Env Biol Fish* 78:333–346
- Johnsson JI, Brockmark S, Naslund J (2014) Environmental effects on behavioral development consequences for fitness of captive-reared fishes in the wild. *J Fish Biol* 85:1946–1971
- Kojima S (1964) Studies on fishing conditions of the dolphin, *Coryphaena hippurus* L., in the western regions of the sea of Japan. VII. Relationship between the stomach contents and the pelagic fauna of juveniles. *Bull Jap Soc Sci Fish* 29:407–414
- Lam CH, Nielsen A, Sibert JR (2008) Improving light and temperature based geolocation by unscented Kalman filtering. *Fish Res* 91:15–25
- Lorenzen K, Beveridge MCM, Mangel M (2012) Cultured fish: integrative biology and management of domestication and interactions with wild fish. *Biol Rev* 87:639–660
- Lu C-P, Wang S-P, Chiang W-C (2019) Analysis of dolphinfish (*Coryphaena hippurus*) population structure in the northwestern Pacific Ocean inferred by mitochondrial DNA sequences. *Proceedings of the 70th Annual Tuna Conference*, Lake Arrowhead, California, May 20–23, 2019
- Martínez-Rincón RO, Ortega-García S, Vava-Rodríguez JG (2009) Incidental catch of dolphinfish (*Coryphaena* spp.) reported by the Mexican tuna purse seiners in the eastern Pacific Ocean. *Fish Res* 96:296–302
- Massuti E, Deudero S, Sanchez P, Morales-Nin B (1998) Diet and feeding of dolphin (*Coryphaena hippurus*) in western Mediterranean waters. *Bull Mar Sci* 63:329–341
- Merten W, Appeldoorn R, Hammond D (2014a) Movements of dolphinfish (*Coryphaena hippurus*) along the U.S. east coast as determined through mark and recapture data. *Fish Res* 151:114–121
- Merten W, Appeldoorn R, Rivera R, Hammond D (2014b) Diel vertical movements of adult male dolphinfish (*Coryphaena hippurus*) in the western central Atlantic as determined by use of pop-up satellite archival transmitters. *Mar Biol* 161:1823–1834
- Merten W, Appeldoorn R, Hammond D (2014c) Spatial differentiation of dolphinfish (*Coryphaena hippurus*) movements relative to the Bahamian archipelago. *Bull Mar Sci* 90:849–864
- Musyl MK, Brill RW, Boggs CH, Curran DS, Kazama TK, Seki MP (2003) Vertical movements of bigeye tuna (*Thunnus obesus*) associated with islands, buoys, and seamounts near the main Hawaiian Islands from archival tagging data. *Fish Oceanogr* 12(3):152–169
- Musyl MK, Domeier ML, Nasby-Lucas N, Brill RW, McNaughton LM, Swimmer JY, Lutcavage MS, Wilson SG, Galuardi B, Liddle JB (2011a) Performance of pop-up satellite archival tags. *Mar Ecol Prog Ser* 433:1–28
- Musyl MK, Brill RW, Curran DS, Fragoso NM, McNaughton LM, Nielsen A, Kikkawa BS, Moyes CD (2011b) Postrelease survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. *Fish Bull* 109:341–368
- Nielsen A, Bigelow KA, Musyl MK, Sibert JR (2006) Improving light-based geolocation by including sea surface temperature. *Fish Oceanogr* 15:314–325
- Olson RJ, Galván-Magaña F (2002) Food habits and consumption rates of common dolphinfish (*Coryphaena hippurus*) in the eastern Pacific Ocean. *Fish Bull* 100:279–298
- Oxenford H, Hunte W (1999) Feeding habits of the dolphinfish (*Coryphaena hippurus*) in the eastern Caribbean. *Sci Mar* 63:303–315
- Palko BJ, Beardsley GL, Richards WJ (1982) Synopsis of biological data on dolphin-fishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linnaeus. *FAO Fish Synop* 130:1–28
- Pérez R, Román A, Glaucó R (1992) Investigation of the reproductive dynamics and preliminary evaluation of landings data of the dolphinfish *Coryphaena hippurus* L. Final report for Dingell-Johnson Project F26-1. Puerto Rico Department of Natural Resources Fishery Research Laboratory, Mayaguez
- Rose CD, Hassler WW (1974) Food habits and sex ratios of dolphin *Coryphaena hippurus* captured in the western Atlantic Ocean off Hatteras, North Carolina. *Trans Am Fish Soc* 103(1):94–100
- Rothschild BJ (1964) Observations on dolphinfish (*Coryphaena* spp.) in the Central Pacific Ocean. *Copeia* 1964:445–447
- Sassa C, Tsukamoto Y, Nishiuchi K, Konishi Y (2008) Spawning ground and larval transport processes of jack mackerel *Trachurus japonicus* in the shelf-break region of the southern East China Sea. *Cont Shelf Res* 28:2574–2583
- Sepulveda CA, Knight A, Nasby-Lucas N, Domeier ML (2010) Fine-scale movements of the swordfish *Xiphias gladius* in the Southern California Bight. *Fish Oceanogr* 19:279–289
- Shcherbachev YN (1973) The biology and distribution of the dolphins (Pisces, Coryphaenidae). *J Ichthyol* 13:182–191
- 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
- Thompson D, Hammond PS, Nicholas KS, Fedak MA (1991) Movements, diving and foraging behaviour of grey seals (*Halichoerus grypus*). *J Zool* 224:223–232
- Wang KY, Liao CH, Lee KT (2008) Population and maturation dynamics of the swordtip squid (*Photololigo edulis*) in the southern East China Sea. *Fish Res* 90:178–186
- Whitney NM, Taquet M, Brill RW, Girard C, Schwieterman GD, Dagorn L, Holland KN (2016) Swimming depth of dolphinfish (*Coryphaena hippurus*) associated and unassociated with fish aggregating devices. *Fish Bull* 114:426–434
- Wilson SG, Lutcavage ME, Brill RW, Genovese MP, Cooper AB, Everly AW (2005) Movements of bluefin tuna (*Thunnus thynnus*)

- in the northwestern Atlantic Ocean recorded by pop-up satellite archival tags. *Mar Biol* 146:409–423
- Wu CC, Su WC, Kawasaki T (2001) Reproductive biology of the dolphin fish *Corphaena hippurus* on the east coast of Taiwan. *Fish Sci* 67:784–793
- Zar JH (2010) Biostatistical analysis, 5th edn. Prentice Hall, New Jersey
- Zúñiga-Flores MS, Ortega-García S, Rodríguez-Jaramillo MDC, López-Martínez J (2011) Reproductive dynamics of the common dolphinfish *Coryphaena hippurus* in the southern Gulf of California. *Mar Biol Res* 7(7):677–689
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