Dolphinfish Movements in the Eastern Pacific Ocean of Mexico Using Conventional and Electronic Tags

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Abstract
Background Dolphinfish, Coryphaena hippurus, are fast-swimming, predatory fish that exhibit fast growth and early maturation. It is an important and potentially renewable recreational and commercial resource throughout their global subtropical to tropical range. While understanding habitat utilization and migratory behavior in these wide-ranging fish is critical to proper regional and international fisheries management, studies have historically relied heavily upon fisheries reported data. This study uses tagging data to explore the vertical and horizontal movements of dolphinfish, focusing on two regions in the Eastern Pacific Ocean (EPO) - west coast of Baja California Peninsula (WBC) and Oaxaca (OAX) coasts of Mexico.

Results Adult dolphinfish (fork length 66 cm - 129 cm) were tagged with conventional (n = 132 tags) and electronic tags (n = 30 tags, miniPAT) between 2010 and 2014. Total recapture rate was 3.7%, and greater for males (5.1%) than females (2.4%). Twenty of 30 deployed electronic tags reported, but all did so before the programmed release date, with days at liberty ranging from 3 to 74 (mean = 42 d). Fish remained within their tagging region with the exception of one fish tagged in WBC which exhibited a large southerly displacement, and one fish tagged in OAX which was recovered to the north. Latitudinal (N-S) and longitudinal (E-W) extents of fish movements increased with days at liberty. In general, fish remained near the surface with short excursions below the isothermal layer but larger OAX fish inhabiting warm waters (sea surface temperatures (SST) > ~26 °C) spent more time below the isothermal layer than smaller fish inhabiting colder waters in WBC (SST > ~22 °C).

Conclusions This study examines the dynamics of the vertical and horizontal movements of dolphinfish. These movements evoke questions about the size-structure of the dolphinfish’s realized thermal niche, its population stock structure, and its spatiotemporal connectivity patterns in the multinational EPO. Longer tag deployments could show larger displacements and observed differences in orientation of seasonal displacement patterns suggest such long-distance movements would provide opportunities for reproductive mixing through trans-national migrations.

Background
The common dolphinfish (Coryphaena hippurus) is an epipelagic predatory fish inhabiting tropical and
subtropical waters in all oceans\(^1\). Globally, dolphinfish constitute non-target catch in large-scale longline and purse seine commercial fishing operations\(^2\), substantial proportions of landings among artisanal fleets\(^3\), and prized catches in regional recreational fisheries\(^4,5\). Although habitat use and distribution patterns define availability and susceptibility to fishing pressure, few studies have reported direct observations of dolphinfish movements and behaviors.

Increasing popularity and global recognition of dolphinfish as an easily accessible, high-protein food item has raised concerns of potential local depletions due to both targeted and incidental fishing throughout its range\(^6\). For example, with the exception of tropical tunas, dolphinfish is the most common species taken when purse seiners set on drifting fish aggregating devices (DFADs), a fishing practice now commonly employed worldwide\(^7\). Due to suspected unreported levels of high incidental catches, taken during purse seine operations and the differing management strategies found throughout its range, dolphinfish was recently listed as a species potentially vulnerable to Illegal, Unreported, and Unregulated (IUU) fishing\(^8\). This listing requires dolphinfish to be traced from point of entry into U.S. commercial entities to point of harvest/production to verify its lawful harvest or production. This recent policy signifies an urgent need to improve the understanding of both dolphinfish landings and the movements that influence connectivity of stocks and breeding populations throughout its distribution, data that are currently lacking\(^8\).

No integrated regional fisheries management plan (FMP) currently exists for dolphinfish in the Eastern Pacific Ocean (EPO), despite the access of eleven countries in the region to this potentially renewable marine resource. These countries, members of the Inter-American Tropical Tuna Commission (IATTC), all land dolphinfish to some degree. In fact, dolphinfish constitute more than half of the large pelagic catch of some member nations\(^3\). However, no comprehensive regional stock assessments for this species have been published to date, which has raised questions about the status of the population in the EPO\(^9,10\) and motivates the need for international agreements on fishing effort and sustainable limits to catch/landings of dolphinfish in the region.
The most comprehensive FMPs and management strategy evaluation in the EPO conducted to date have been in the southern EPO\textsuperscript{10,11}. Ecuador established an annual closure from July 1 to October 7, prohibiting the capture of fish less than 80 cm in total length, applying fleet size restrictions, and requiring real-time observation and reporting in 10\% of Ecuador’s longline fleet\textsuperscript{3,12}. In Peru, authorities implemented a seasonal closure from May 1 to September 30 and a minimum size limit of 70 cm fork length\textsuperscript{13}. These national management plans are positive initiatives designed to improve the conservation of the species in the southern EPO, but comparable plans do not exist from Colombia northward to the United States; however, low population structure\textsuperscript{14,15} likely results in some measure of correspondence in seasonal abundance patterns and movements of dolphinfish between nations. Better information on fishing, landings and movement ecology is required to aid the development of effective national and multi-national resource management throughout the dolphinfish’s range in the EPO.

Globally, dolphinfish are known to undertake long-distance seasonal migrations within home ranges limited poleward by the 20 °C surface isotherm to the north and south\textsuperscript{16}. In the Atlantic, electronic and conventional tagging and genetic studies suggest that dolphinfish are regionally connected in an annual western/central Atlantic migration circuit, based on low population structure between sampled sites and observed movements between locations\textsuperscript{4,5,17}. Additional studies have documented that dolphinfish strongly associated with floating surface macroalgae, flotsam, and Fish Aggregating Devices (FADs), with both homing and high levels of fidelity (> 15 days) observed in the Indian Ocean\textsuperscript{18–23}. A study combining commercial and recreational fisheries data determined that while sea surface temperature is a strong correlate of dolphinfish catch, chlorophyll-a is not\textsuperscript{24}.

In terms of vertical movements, short duration tagging studies in both the western central Atlantic and western Pacific Oceans report diel shifts in behavior from shallow depths during the day to deeper depths (i.e., below the isothermal layer) at night, likely in response to movements of aggregating epipelagic and mesopelagic prey, or to reduce risk of predation\textsuperscript{25,26}. The same diel
vertical behavior was noted in both farm-reared and wild dolphinfish in marginal waters of the East China Sea\textsuperscript{27}. In the oceanic waters of the EPO, long term observations of horizontal and vertical movements of dolphinfish have not been described to date.

Patterns of dolphinfish fishing effort and catches are markedly seasonal within the EPO. Peak abundances in South America fisheries (Peru and Ecuador) occur from October to April (austral spring-summer)\textsuperscript{3,28}, while peak abundances occur from September to November in Baja California Sur (boreal summer-autumn)\textsuperscript{29}. Seasonal latitudinal movements apparently correspond with physical changes in oceanic conditions, e.g. northerly range extensions beyond the coast of Baja California Norte to as far north as Oregon, U.S. in warm El Niño years\textsuperscript{30,31}. While it has been suggested that the migratory behaviors of dolphinfish are related to sea surface temperature\textsuperscript{1,32}, this relationship has not been analyzed in detail anywhere within the EPO. Behavioral responses to changing surface currents, temperature regimes and/or prey abundance patterns may influence both short-term movements and long-term migrations of this active, epipelagic predator.

The research presented here is motivated by the increasing need to better manage the population of dolphinfish in the entire EPO. Due to their high growth rates and fecundity, properly managed dolphinfish fisheries are a potentially renewable, stable protein resource for many nations of the Americas. By investigating dolphinfish movements within the Mexican portions of the EPO, and the possible timing and routes of migrations that may connect dolphinfish breeding stocks, this study aims to increase the resolution of the realized thermal niche within and beyond the broad, long-established range of sea surface temperature (20–30 °C)\textsuperscript{16}. By investigating movements as they relate to changes in water temperature, this study provides insights into habitat availability as well as the potential for inter-regional mixing.

As electronic tagging-based technologies continue to develop, improving end-user interpretation of products offered by widely used tag manufacturers remains valuable to scientists. New analytical approaches are reported here that may apply to electronic tag-based investigations of many marine epipelagic fishes. Specifically, a novel method is described for evaluating the proprietary daily global
positions ("geolocations") produced by WC-GPE3, a new online algorithm provided to end-users by tag manufacturer Wildlife Computers→.

Despite the commercial, recreational and artisanal importance of the dolphinfish fishery in the EPO, there is great uncertainty about the status of the species and the presence of population structure in the region6. The many fisheries that compete for this resource do so at various scales of intensity. Advancing regional knowledge of dolphinfish movements will help improve its management within Mexico and provide foundational underpinnings for an integrated EPO-wide fisheries management plan.

Results
Deployments, Recoveries and Tag Performance
A total of 162 tags (30 electronic and 132 conventional) were deployed on dolphinfish from 2010–2014 in oceanic waters off the coast of Mexico. Four tagging trips took place late summer/early fall offshore the west coast of Baja California Peninsula (denoted WBC, hereafter) and two late winter/early spring trips were undertaken offshore of the Mexican state of Oaxaca (OAX, hereafter) (Fig. 1; Table 1). Ninety-four percent of all tags were deployed in WBC (fork length range: 66 cm – 112 cm) with the remaining six percent deployed in OAX (100 cm – 129 cm; Table 1, Fig. 3).

Table 1

| Date          | Map Location | Number of Total Fish Tagged (Electronic Tags) | Number of Fish Recaptured (Reported) |
|---------------|--------------|---------------------------------------------|--------------------------------------|
|               |              | Total | Females | Males | Total | Females | Males |
| WBC           |              |       |         |       |       |         |       |
| Sep 30–Oct 4, 2010 | 1 | 152 (20) | 81 (9)  | 71 (11) | 6 (12) | 1 (5)  | 5 (7)  |
| Sep 29, 2011  |              | 83 (5) | 60 (4)  | 23 (1)  | 0 (5)  | 0 (4)  | 0 (1)  |
| Jul 20, 2013  |              | 59 (5) | 18 (2)  | 41 (3)  | 6 (0)  | 1 (0)  | 5 (0)  |
| Sep 21–29, 2014 | 4 | 6 (6)   | 1 (1)   | 5 (5)   | 0 (5)  | 0 (1)  | 0 (4)  |
| OAX           |              | 4 (4) | 2 (2)   | 2 (2)   | 0 (2)  | 0 (0)  | 0 (2)  |
| Mar 6–7, 2013 |              | 10 (10) | 2 (2) | 8 (8) | 1 (8) | 0 (2) | 1 (6) |
| Feb 11, 2014  |              | 4 (4) | 0 (0) | 4 (4) | 1 (4) | 0 (0) | 1 (4) |

All fish in the study were mature adults according to published length at maturity data33. Sex ratios of
tagged fish were fairly even overall, with 79 males and 83 females tagged (0.95:1); however, more males (19 fish) than females (11 fish) were tagged with electronic tags (1.7:1). Although previous studies have shown sex-dependent length frequency distributions\textsuperscript{33}, female fish did not differ significantly in size (median: 88 cm [IQR: 83.3–93]) from the male fish tagged in this study (89 cm [82–93], Wilcoxon Rank-Sum, \( p = 0.96 \)). However, there were regional differences in size as fish with reporting electronic tags in WBC were significantly smaller (95 cm [92 cm – 101 cm]) than those tagged with electronic tags in OAX (102 cm [98–112], Wilcoxon Rank-Sum, \( p = 0.02 \), Fig. 2).

Overall, 4.3 percent of all tags were recovered and 67 percent of electronic tags reported; however, recovery rates and tag performance varied by year and by sex (Table 1). Males were twice as likely to be recaptured than females; however, there was no difference in electronic tag reporting rates between males and females (Table 1). One of the deployed electronic tags did not report, but its numbered leader (#5015 in Table 2) was recovered, thus counting as a conventional tag recovery and a non-reporting electronic tag. One fish is represented twice in Table 2, as its electronic tag (#111535) reported before the fish and its conventional tag (#5056) were recaptured. All mini-PATs popped off prior to their programmed release date with days at liberty ranging from 4 to 62 days (mean = 24 days). These deployment times for electronic tags were shorter on average than for recovered conventional tags which ranged from 15 to 141 days (mean = 56 days). Deployment duration for both conventional and electronic tags did not correlate with fish length (Pearson Correlation, \( p = 0.58 \)), sex (Wilcoxon Rank-Sum, \( p = 0.53 \)), or region (Wilcoxon Rank-Sum, \( p = 0.28 \)).

Due to reduced deployment durations from premature releases, temporal coverage of the electronic tagging data is limited to the months of July – October in WBC and February – March in OAX.
Table 2
Deployment and recapture information on the west coast of Baja California Peninsula (WBC) and Oaxaca (OAX), Mexico. Conventional tags are denoted with an asterisk.

| Tag Number | Deploy Date | Days at Liberty | Fork Length (cm) | Sex (F:M) | Disp. Rate (km d$^{-1}$) | Estimated Speed (km d$^{-1}$) | Total Disp. (km) |
|------------|-------------|-----------------|------------------|----------|---------------------|-----------------------------|-----------------|
| WBC Fish   |             |                 |                  |          |                     |                             |                 |
| 62142      | 02-Oct-10   | 29              | 93               | F        | 14                  | 15 [7, 25]                  | 400             |
| 62143      | 02-Oct-10   | 25              | 90               | F        | 15                  | 13 [8, 25]                  | 384             |
| 62145      | 03-Oct-10   | 4               | 95               | F        | 45                  | 59 [32, 84]                 | 181             |
| 62147      | 03-Oct-10   | 13              | 91               | M        | 15                  | 12 [5, 24]                  | 200             |
| 62148      | 03-Oct-10   | 9               | 95               | F        | 8                   | 6 [3, 18]                   | 73              |
| 806*       | 29-Sep-11   | 39              | 89               | M        | 17                  | -                           | 675             |
| 812*       | 29-Sep-11   | 15              | 82               | M        | 58                  | -                           | 866             |
| 823*       | 29-Sep-11   | 74              | 86               | M        | 12                  | -                           | 866             |
| 824*       | 29-Sep-11   | 65              | 86               | M        | 13                  | -                           | 866             |
| 829*       | 29-Sep-11   | 28              | 94               | F        | 24                  | -                           | 675             |
| 5015*      | 29-Sep-11   | 29              | 102              | M        | 14                  | -                           | 406             |
| 111522     | 20-Jul-13   | 57              | 100              | M        | 13                  | 29 [16, 48]                 | 734             |
| 111524     | 20-Jul-13   | 26              | 106              | M        | 15                  | 32 [23, 58]                 | 377             |
| 111525     | 20-Jul-13   | 44              | 98               | F        | 4                   | 29 [16, 59]                 | 154             |
| 111532     | 20-Jul-13   | 8               | 93               | M        | 36                  | 55 [43, 72]                 | 290             |
| 111533     | 20-Jul-13   | 8               | 90               | M        | 17                  | 81 [38, 108]                | 138             |
| 111534     | 29-Sep-14   | 7               | 102              | M        | 25                  | 15 [6, 55]                  | 174             |
| 132984     | 29-Sep-14   | 5               | 112              | M        | 23                  | 33 [19, 78]                 | 114             |
| All WBC    |             | 26              | 94 [90, 100]     | (6:12)   | 15 [13, 24]         | 29 [14, 38]                 | 381 [176, 675] |
| OAX Fish   |             |                 |                  |          |                     |                             |                 |
| 5056*      | 06-Mar-13   | 141             | 113              | M        | 11                  | -                           | 1,574           |
| 111531     | 06-Mar-13   | 7               | 100              | M        | 31                  | 72 [59, 90]                 | 222             |
| 111535     | 06-Mar-13   | 13              | 113              | M        | 25                  | 42 [11, 68]                 | 327             |
| 111528     | 07-Mar-13   | 12              | 120              | M        | 30                  | 22 [8, 62]                  | 367             |
| 111530     | 07-Mar-13   | 5               | 115              | M        | 53                  | 19 [17, 58]                 | 265             |
| 128931     | 11-Feb-14   | 54              | 103              | M        | 10                  | 28 [14, 54]                 | 539             |
| 128932     | 11-Feb-14   | 42              | 118              | M        | 4                   | 19 [6, 48]                  | 147             |
| 128934     | 11-Feb-14   | 47              | 107              | F        | 8                   | 30 [16, 67]                 | 378             |
| 128936     | 11-Feb-14   | 62              | 113              | F        | 5.4                 | 27 [14, 56]                 | 335             |
| All OAX    |             | 42 [12, 54]     | 113 [107, 115]   | (2:7)    | 11 [8, 31]         | 28 [21, 33]                 | 335 [265, 378] |

Horizontal and Vertical Behaviors
Conventional tag recoveries from longer duration deployments showed fish movements out of the tagging region (6 out of 7 recoveries); while electronic tags generally reported from shorter deployments on fish that remained within the original tagging area – with the exception of 111522 (Fig. 4). Net displacements between deployment locations and recovery sites ranged from 73.3 km to 1574 km (mean = 434 km). Location estimations (see methods for description of techniques using WC-GPE3) had the highest scores (i.e., best sea surface temperature data agreement between tag observations and those derived from model locations) when the initial animal speed input parameter ranged from 1.75 m s$^{-1}$ to 3.75 m s$^{-1}$ (3 m s$^{-1}$ [2.5 m s$^{-1}$, 3.31 m s$^{-1}$]). The initial input parameter does not dictate the daily speeds, but rather provides an envelope of speeds available to the model.
Median estimated daily displacements along the estimated tracks ranged from 6.1 to 80.8 km d\(^{-1}\) (Table 2). Overall displacement rates (from deployment location to recovery location, including conventional tags) ranged from 3.50 to 57.71 km d\(^{-1}\).

Standardized by body length, daily speeds did not significantly vary by region (Wilcoxon Rank-Sum, \(p = 0.79\)) or by sex (Wilcoxon Rank-Sum, \(p = 0.34\), Table 2). Latitudinal and longitudinal extent of displacements differed as a function of days at liberty and region (Fig. 5). All fish exhibited an expansion of their latitudinal habitat range with more days at liberty, with WBC fish having a greater range in latitude with longer deployment lengths (Pearson Correlation, OAX: slope = 0.04, \(p = 0.003\); WBC: slope = 0.06, \(p = 0.0006\)). Fish from both regions showed greater increases in longitudinal range with longer deployment lengths (Pearson Correlation, OAX: slope = 0.08, \(p = 0.0004\); WBC: slope = 0.08, \(p = 0.001\)).

The vast majority of depth related behavior was restricted to surface waters, with 68.9 percent of total reported time-series observations (140,042 of 203,264) occurring in the shallowest 5 m. For most fish, daily median depths were shallower than 5 m for the majority of their time at liberty (Table 3). In general, WBC fish spent a greater percentage of time in the top 5 m (84.6% [61.6%, 94.1%]) and dove to greater daily maximum depths (59 m [39 m, 84.5 m]) than OAX fish (61.1% [35.1%, 88.5%]; 36.5 m [26.5 m, 45 m]), Wilcoxon Rank-Sum, \(p < 0.001\).
Table 3
Statistical summary of vertical behavior. Fish with statistically different behavior between day and night (p < 0.05, Wilcoxon Sign-Rank test) are in bold.

| Fish ID | Number of Full Days | Median Depth (m) | Maximum Depth (m) | Inter-quartile Depth Range (m) |
|---------|---------------------|------------------|-------------------|------------------------------|
|         | Day | Night | Day | Night | Day | Night | |
| WBC     | 139 | 1[2]  | 1[5] | 46[23, 80] | 37[6, 65] | 1[6]  | 1[20] |
| 62142   |     | 27[3, 19] | 1[3] | 40[32, 80] | 12[6, 67] | 8[5, 20] | 1[14] |
| 62143   | 24  | 1[3]  | 3[1, 42] | 85[76, 93] | 65[5, 78] | 6[0, 54] | 19[0, 38] |
| 62145   | 3   | 2[2, 2] | 31[9, 33] | 91[79, 105] | 77[65, 92] | 3[2, 3] | 14[7, 17] |
| 62147   | 12  | 1[1, 2] | 1[1, 4] | 57[34, 74] | 39[4, 52] | 1[1, 2] | 1[1, 15] |
| 62148   | 8   | 2[2, 2] | 2[2, 2] | 32[11, 43] | 9[3, 37] | 1[1, 1] | 1[1, 1] |
| 111522  | 17  | 1[1, 1] | 4[1, 8] | 23[19, 39] | 57[40, 70] | 0[0, 1] | 22[7, 37] |
| 111524  | 7   | 1[1, 1] | 1[1, 1] | 41[29, 84] | 39[7, 48] | 1[1, 2] | 1[1, 9] |
| 111525  | 17  | 1[1, 1] | 1[1, 1] | 52[42, 82] | 28[2, 37] | 1[1, 1] | 1[1, 1] |
| 111532  | 7   | 2[1, 2] | 13[1, 22] | 43[29, 60] | 66[26, 73] | 1[1, 4] | 21[1, 32] |
| 111533  | 7   | 1[1, 1] | 1[1, 1] | 51[39, 57] | 29[29, 38] | 2[1, 2] | 1[1, 9] |
| 111534  | 6   | 1[1, 1] | 1[1, 1] | 1[1, 1] | 2[1, 1] | 1[1, 1] | 1[1, 1] |
| 132984  | 4   | 1[1, 1] | 1[1, 1] | 1[1, 1] | 1[1, 28] | 0[0, 0] | 0[0, 1] |
| OAX     | 164 | 1[1, 16] | 3[1, 18] | 30[11, 39] | 34[23, 40] | 3[1, 11] | 9[1, 16] |
| 111528  | 10  | 1[1, 9] | 1[1, 6] | 1[1, 39] | 1[1, 35] | 1[1, 15] | 1[0, 10] |
|         | 4   | 1[1, 8] | 9[1, 21] | 12[1, 27] | 17[1, 46] | 6[0, 14] | 5[0, 17] |
|         | 6   | 1[1, 1] | 1[1, 1] | 1[1, 1] | 1[1, 1] | 1[0, 0] | 1[0, 4] |
|         | 1153  | 1[1, 1] | 1[1, 1] | 2[1, 2] | 2[2, 2] | 1[1, 1] | 1[1, 1] |
| 128931  | 38  | 24[9, 27] | 20[16, 24] | 37[34, 42] | 35[29, 40] | 7[5, 12] | 11[7, 17] |
| 128932  | 29  | 1[1, 16] | 1[1, 4] | 31[24, 37] | 32[26, 37] | 3[1, 10] | 14[1, 17] |
| 128934  | 32  | 1[1, 1] | 1[1, 10] | 28[16, 38] | 29[22, 39] | 1[0, 8] | 9[0, 16] |
| 128936  | 34  | 1[1, 11] | 2[1, 16] | 27[22, 36] | 37[31, 46] | 4[0, 15] | 11[0, 18] |

Diving behavior varied significantly, with fish exhibiting greater dive activity and depth during the day than at night as well as the opposite pattern (for example: Fig. 6). Overall, maximum daily depth was significantly greater during the day than at night for WBC fish, whereas OAX fish did not exhibit significant diurnal difference in diving behavior (Table 3). Although WBC fish exhibited deeper maximum daily diving depths, the variance in daily diving depths – measured here as the - daily interquartile range – was greater in the OAX fish (10.1 [0.5, 17]) than the WBC fish (1.5 [0.5, 14]; Wilcoxon Rank-Sum, p = 0.03). In both regions, most dolphinfish showed more variance in daily diving depths at night than during the day (Table 3).

Thermal Habitat
Thermal habitat availability differed between the two regions during the respective tagging deployments. In OAX, sea surface temperatures are warmer throughout the year than in WBC (Fig. 7a). In WBC, the lowest sea surface temperatures occur in February through March while the highest occur in August through October. On the other hand, OAX does not exhibit a strong annual cycle; sea surface temperatures are relatively stable intra-annually between 26 °C and 31 °C.
Vertical thermal habitat availability also differs between the regions. The isothermal layer depth in WBC was twice as deep as that in OAX (Fig. 7b). These regional patterns resulted in significantly different thermal habitats for fish in WBC versus OAX, with WBC fish experiencing colder sea surface temperatures and deeper isothermal layers than OAX fish (Table 4). However, the timing of tag deployments had the effect of minimizing observed differences in sea surface temperatures between the two regions (Fig. 7a).

Differences in depth related behaviors corresponded with differences in thermal habitat availability between regions. As a result of these regional differences, OAX fish experienced significantly warmer median daily temperatures (27.2 °C [26.2 °C, 28.2 °C]) than WBC fish (22.4 °C [22 °C, 23.1 °C], Wilcoxon Rank-Sum, p < 0.001) even though fish in both regions spent most of their time within the isothermal layer (Table 4). Observed median daily temperatures tracked sea surface temperatures, but fish in OAX recorded lower median daily temperatures in waters with sea surface temperatures higher than approximately 26 °C (Fig. 8a). Lowest minimum experienced temperatures were directly correlated with low sea surface temperatures (Pearson coefficient, p < 0.001, Fig. 8b). Fish in OAX spent less time at the surface than fish in the WBC, and this correlates with differences in SST – with fish exhibiting less surface oriented behavior in waters with SST greater than 26 °C (Fig. 8c).

**Discussion**

This study reports the horizontal and vertical activity of mature dolphinfish observed through the use of conventional tags and PSATs in the EPO off west coast of Baja California Peninsula and Oaxaca, Mexico. Fish sizes, as measured by fork length, were similar for males and females, but larger fish were tagged in the OAX than in the WBC. Alejo-Plata, et al.\(^\text{\ref{Alejo}}\) provided evidence of seasonal sex-based segregation in OAX, finding sex ratios skewed to more females than males in Apr-May and more males than females in Nov-Dec. Higher tag recapture rates of male dolphinfish in this study suggest that males may be more susceptible to fisheries than females. Possible explanations for the observed recapture difference may be a matter of market preference for “bulls”, post capture release of gravid females or increased electronic tag shedding (and loss) by more active females; however, this result may be a random effect due to the relatively small sample size.
While premature release of electronic tags resulted in observations of limited geographic movements, the potential for longer migrations is discernible. In general, WBC dolphinfish moved primarily latitudinally (N-S), whereas OAX fish moved longitudinally (E-W) over the course of the study, with only two fish – one from WBC and one from OAX – observed moving between the two regions. The land mass of mainland Mexico limits latitudinal movements to the north of dolphinfish tagged in OAX; however, reciprocal southerly movements, where no such boundary exists, were not observed. Thus, the axis of movements is due to either available thermal habitat, surface currents, the presence of shallow oxygen minimum layers, or a combination of factors making the habitat less suitable to the south of OAX than to the west.

For either WBC tagged in late Summer and Fall, or OAX fish tagged in early Spring, connectivity between regions over the durations of electronic tag deployments was not observed, but daily movements indicated southerly tendencies during summer and autumn for WBC fish and westerly tendencies from early to late spring for OAX fish. Several WBC fish appeared to have moved south in response to seasonal sea surface temperature changes as the tags released and one fish from OAX was recaptured in WBC in summer after a premature pop-off in spring. As there was a correlation between tagging durations and displacement in fish from both regions, extension of these movements over longer tagging durations may indeed show connectivity between these areas as indicated by conventional tags.

Dolphinfish exhibited a variety of diving behaviors that correlated more with region than with sex or size. Fish from both regions were observed more frequently in shallow depths but also made frequent shallow dives, and occasional deep dives to below 100 m with maximum depth of 262 m. As reported in other studies, shallow marine habitat use may be attributed to prey location\textsuperscript{34,17}, association with flotsam\textsuperscript{35} (such as tree trunks, sargassum spp mats, which commonly occur throughout the study region), or bioenergetic conservation by remaining in preferred thermal conditions\textsuperscript{25,36}. Generally, when not within the top five meters of the surface layer, dolphinfish most often occupied depths within the isothermal layer.
Although only reverse diel diving behavior has been observed in other studies\textsuperscript{25,36,17,27,26}, this study observed both traditional and reverse diel diving behavior. This plasticity in habitat utilization patterns was similar in fish across regions and sexes, and thus may be a result of ephemeral differences in the thermal structure of the water column, presence or absence of predators, and/or changes in the distribution and availability of prey items. It is also possible that longer duration tag deployments in this study reveal a behavioral plasticity and variability not observed in studies with short tag deployments.

Changes in degree of surface orientation (e.g. basking) suggest that some diving and migratory behaviors may be in response to regional scale differences in thermal habitat. Fish in the WBC region experienced significantly colder surface waters and deeper isothermal layer depths than fish in the OAX. This correlated with more surface oriented behavior and deeper dives in the WBC fish than in the OAX fish. Furthermore, fish in the OAX that experienced waters with sea surface temperatures greater than 26 °C spent more time at depth, perhaps to reduce their experienced median water temperature. These behavioral switches may limit the realized ecological niche space of dolphinfish and may drive migratory behaviors between the two regions, for example, when the waters in the WBC region seasonally cool during boreal winter months (not observed in this study).

These temporally limited observations support published dolphinfish distribution models based on fisheries dependent catch data in the region. Marín-Enríquez et al.\textsuperscript{37} modeled the probability of dolphinfish occurrence in this region from incidental catch data taken from tuna purse seine fisheries as a function of different environmental parameters. The study predicted dolphinfish occurrence in greatest abundances in a distant offshore oceanic zone of the EPO during late spring, an area that extended northeastward through summer to the west coast of Baja California peninsula. Peak abundance off WBC occurred annually in summer and fall several months after intense winter and spring upwelling occurred allowing dolphinfish’s preferred prey (pelagic red crab, Pleuronocodes planipes) and optimal thermal conditions (23–28 °C) to establish. Dolphinfish were modeled to retract from the WBC region later in the year when cold water upwelling events returned.
This seasonal abundance pattern in WBC is also supported by dolphinfish catch rates by the Los Cabos sportfishing fleet, which have been reported to be higher west of the capes of the Baja California Sur during September\textsuperscript{38}. Additional support can be found in the catch statistics from the south of Cabo Corrientes, which have been shown to be maximal in the fourth quarter of the year\textsuperscript{39}. Less information is available for nearshore and offshore areas of the OAX region, as it appears to be a gap in commercial and recreational fishing or reporting, perhaps due to its remoteness and lack of accessibility to ports and populations.

**Conclusions**

This study provides new information on the dynamic behaviors of dolphinfish in the EPO while supporting previously reported large-scale thermal habitat constraints to dolphinfish abundance and distribution patterns. While orthogonal geographic axes of movement (N/S versus E/W) provide evidence on which to base hypothetical mixing routes, regional differences in thermal structure present environmental variability (and corresponding changes in diving behavior) to migrating fish. However, temporal limitations in tracking durations and high uncertainty bounding daily geolocation estimates restrict analysis of potential migration routes within or beyond the study region. Improvements in tag retention are critical to obtaining deployment lengths that span summer and winter months, when region-connecting migrations may occur.

The new geolocation algorithm used in this study, WC-GPE3, allowed the incorporation of uncertainty into model selection and geolocation estimation. The methodology provided here is critical to this study, and useful to future WC-GPE3 users, but is substantially a sensitivity test of a single model for a single species. As advances in geolocation algorithms continue to be made, accuracy-based error estimates, though difficult to obtain and often limited in sample size or conditions, are as necessary as precision-based likelihoods. In addition, comparison of the various available geolocation model outputs (for example, see Braun\textsuperscript{40}) along with estimates of their respective accuracy bounds is important area of research. Finally, increasing the cost effectiveness of GPS based electronic tags is perhaps a more favorable way to solve the “track-finding” problem of light-based geolocation\textsuperscript{41,42}. 
Future population and movement studies of dolphinfish in the EPO should strive to provide data necessary to improve the international management of the species as a potentially renewable natural and economic resource. Our data indicate that dolphinfish behaviors may differ between distant global habitats such as the northwest Atlantic and Pacific Oceans, but also within subregions of the EPO\textsuperscript{4,25}. These differences may be indicative of stock structure and reproductive isolation, but are insufficient as proof of such. More directed and geographically diverse studies are needed to establish or refute reproductive connectivity of dolphinfish within and between the eleven EPO nations that exploit dolphinfish and other large marine predators economically.

Considering the economic importance of dolphinfish as a resource throughout Baja Mexico, mainland Mexico and Central America, it is important to note the migration of dolphinfish out of the WBC region as indicated by five conventional tag recaptures more than 500 km away from their tagging locations, and one out of the OAX region, a 1500 km displacement (Figure 4, Table 2). It is imperative that actual migration routes, inclusive of dates of regional exit and entry, be determined by future studies that emphasize increasing the duration of electronic tag deployments (for example, see Perle\textsuperscript{43}). Oceanic migration routes may introduce dolphinfish to unregulated fishing pressure in international waters or those of other EPO nations or alternatively provide them with escapement from intensive coastal fishing. Understanding long-distance, directed migrations would also help scientists determine if a single, panmictic population of dolphinfish exists in the EPO.

Finally, if prey availability predicts dolphinfish behaviors along with water column thermal characteristics within a region, improved information on forage fish abundance and distribution is needed to predict their small-scale movements. Our tag recovery data also suggest that adult dolphinfish may be ecologically important prey for larger fish, as well as important consumers of small forage species. Epipelagic feeding strategies expose dolphinfish to recreational sport fishing vessels and other larger marine predators, while deeper feeding strategies expose them to different types of commercial gear. A greater understanding of where and when these behaviors prevail would help in the regulation of their capture and the maintenance of their abundance locally, regionally and
globally.

Methods

**Fishing and Tagging Protocol**

To assess dolphinfish behavior and habitat preferences in the EPO waters of Mexico, fish were tagged in two regions: offshore of west coast of Baja California Peninsula (WBC: 20 - 35° N, 110 - 118.0° W) and farther south in the coastal waters of Oaxaca, Mexico (OAX: 10 - 18° N, 85 - 100° W; Figure 1, Table 1). Dolphinfish tagging in WBC occurred in conjunction with the Monterey Bay Aquarium’s Animal Care Division field collection trips. Although adult dolphinfish were targeted in both regions, fishing methodology differed as a result of available fishing vessels and local expertise. Tag models and tag applications were consistent in both regions – with the exception of modifications to improve tag retention in the fall of 2014.

Dolphinfish were caught either by rod and reel (WBC) or longline (OAX). Rod and reel fishing targeted dolphinfish associated with floating kelp. The fishing rigs included Seaguar® 25-40 lb. test monofilament and Owner® circle-style hooks (size 1/0) baited with live sardines (*Sardinops sagax*).

Longlines were set according to local practices by participating artisanal fishermen aboard small pangas, spanned approximately 5 km in total length and soaked for 7 hours with checks every 2 hours. Hooks were baited with a mix of live jacks (4-6 cm; Family Carangidae) or pieces of black skipjack (*Euthynnus lineatus*).

Upon capture, dolphinfish selected for tagging were either landed onboard the vessel with a nylon sling (WBC) or held tightly alongside the panga (OAX). To minimize stress in the landed fish, their eyes were covered with a wet towel, and gills irrigated with oxygenated seawater to minimize stress. In both areas, the tagging procedure lasted 3-5 minutes.

Fish were tagged with conventional, plastic dart tags (Floy Tag Inc., Seattle, Washington, USA) and/or with electronic pop-up satellite tags (MiniPAT, Wildlife Computers Inc., Redmond, WA, USA), generally according to size with fish larger than 90 cm considered for electronic tagging. For the majority of the study, conventional and electronic tags were inserted into the dorsal musculature of smaller fish to the depth of pterygiophores. While conventional tag application was unaltered through the study,
electronic tag application in WBC in fall 2014 was changed from previous deployment years to improve tag retention and, therefore, deployment duration.

Prior to fall 2014, the electronic tags were attached to nylon anchors with numbered, shrink-wrapped 300 lb. (136 kg) test monofilament leaders and inserted into the dorsal musculature as described above. However, in fall 2014, this design was altered (following Merten et al.⁴). The new method included a 300 lb (136 kg) monofilament leader (Momoi® extra hard), 40 cm in length, anchored to each tag with an appropriately sized stainless-steel crimp. The unattached end of the monofilament leader was inserted into a 15.2 cm long hollow stainless steel, cannula (.125 cm OD, .093 ID) with 45° beveled sharp edge. After a small incision was made midline above the spine and below the dorsal ridge with a surgical scalpel, the applicator tube was used to push the leader entirely through the fish anteriorly from the point of insertion at an angle of 45°, parallel to the midline of the fish. After the monofilament leader passed through the fish, it was anchored to the tag leader with another stainless-steel crimp and two affixed ½ inch diameter, circular laminated vinyl backing plates (Floy Tag®). This resulted in a small loop around the dorsal musculature of the dolphinfish with approximately ~4 cm of monofilament leader between the electronic tag and fish.

*Electronic Tag Programming Protocol*

Electronic tags were programmed to release from the fish by corroding a sacrificial link after either 60 or 90 days. During deployment, electronic tags recorded depth, ocean temperature and light at 3 second intervals. However, complete archival records are only available if a tag is physically recovered and capable of being downloaded. During this study, no electronic tags were physically recovered. Therefore, archived data onboard tags, either subsampled or summarized for post-release transmission via satellite, were accessed via the Wildlife Computers® data portal (mywildlifecomputers.com). Data strings of temperature and depth time-series were subsampled from the archival data and transmitted in packets of ten data points per 150 seconds; binned summaries of time-at-depth [0,5,10,15,20,30,40,50,75,100,150,>150 meters] and time-at-temperature [4,16,18,20,22,24,26,27,28,29,30,>30 °C] used 12 bins to bound and center fish depth and
temperature utilization, respectively. Light and mixed layer temperature daily summaries were transmitted using default settings. Transmission priorities were set to favor the light data necessary for geolocation (WC-GPE3). Statistical analyses reported here are restricted to the transmitted time-series data and were conducted in the MATLAB computing environment (MATLAB, 2016).

To assess survivorship and tag performance, recoveries, reporting rates, and early releases were calculated as a function of region, sex, and size. Tags that did not report may have failed due to one of several undiscernible events – e.g., tag/battery failure, user error upon deployment, recovery by fishermen with subsequent intentional or unintentional disabling of transmitting capability, growth of fouling organisms that impact antenna or wet/dry sensor orientation, or animal mortality causing rapid sinking of the tag to destructive depths in deep ocean waters. Tags reporting early may be the result of “tag-shedding”, animal or tag predation resulting in free floating tags, or behavior-based triggering of early release logic (e.g. extended surface orientation). Extensive analysis of factors impacting tag reporting success are interesting, but beyond the scope of this report.

**Behavioral Analysis**

Semi-daily estimated geographic positions (“geolocations”) for electronic tags were calculated using proprietary software (“WC-GPE3”) from tag manufacturer, Wildlife Computers®. WC-GPE3 employs a state-space model to incorporate information from tags (i.e., light curves and surface temperature), satellites (i.e., surface temperature), and an animal movement (speed) model to create a grid of position likelihoods at a spatial resolution of 0.25 degrees\textsuperscript{44}. Based on the high-performance swimming of dolphinfish\textsuperscript{45,46}, WC-GPE3 was run with animal speeds from 1 m/s to 5 m/s at increments of 0.25 m/s. Best model runs were chosen as those model that (i) produced the lowest areas of uncertainty and (ii) had overall scores above cut-off criteria ($s_{crit}$):

\[ s_{crit} = 0.95 \left( s_{max} - s_{min} \right) + s_{min} \]

where $s_{max}$ is the maximum score and $s_{min}$ is the minimum score (Figure 8). Area of uncertainty was calculated as the area of the grid cells that contained 95% of the cumulative uncertainty per
observation, excluding the first and last days of deployment. Scores were generated internally by WC-GPE3 and represent the average fit of the tag’s observations (tag light curves and sea surface temperature) with those of the model-derived locations (pers. comm., Suzanne Kohin).

Trends in overall horizontal movements were examined as both total displacements and estimated speeds. Daily displacement rates (km d\(^{-1}\)) were calculated according to geodesic straight-line (great circle) distance and days at liberty between release and recapture/pop-up locations for conventional and electronic tags, respectively. For geolocations, daily speeds (km d\(^{-1}\)) were estimated using the centroid of the daily area of uncertainty. These speeds were summarized and presented as median [25\(^{th}\) percentile, 75\(^{th}\) percentile] unless otherwise stated. Patterns in habitat extent or range – measured by range of latitude (or longitude) as a function of days at liberty – were examined for potential of migration or mixing between the two regions.

Maximum and median depth were calculated per day observed. Depth range of the vertical habitat was also calculated as the interquartile range of daily depths. Proportion of time basking was estimated as the proportion of daytime observations in the upper 5 m. Because dolphinfish have been shown to exhibit diel diving behavior in the western central Atlantic\(^4\), diving behavior was also examined diurnally. Nighttime and daytime hours were determined using tag recorded and transmitted light curves, and the hour around sunrise and sunset were excluded. Significance of diurnal comparisons was evaluated using the Wilcoxon Sign-Rank test.

Analyses were conducted per fish and patterns in fish dive behavior were examined within the context of tagging region. As there are gaps in the temperature and depth time-series, diurnal behavior was only examined in 24-hour periods where there were depth data for greater than 50% of each day and night. Values are presented as median [25\(^{th}\) quartile, 75\(^{th}\) quartile] unless otherwise stated. When comparing across regions, daily values were used to capture variability both among and within fish. Significance of differences between regions was determined using the Wilcoxon Rank-Sum test unless otherwise stated.
Analysis of Thermal Habitat

A main focus of this study is to place observations of movements within the context of the animal’s utilization of the available thermal habitat. Thermal habitat utilization was characterized by daily median, minimum and sea surface temperatures determined via electronic tagging data. The percent time in the isothermal layer – ILD, defined as the maximum depth at which the water temperature remains within 0.8 °C of the sea surface temperature (average temperature of the top 5 meters\textsuperscript{47}) – was calculated per fish for both day and night. Thermal habitat utilization of OAX fish and WBC fish was then compared using the Wilcoxon Sign-Rank test. Thermal habitat utilization for a day was only determined if data for greater than 50% of the day was reported (as with depth data).

To assess thermal habitat availability, sea surface temperatures were compiled for the time period of this study (2010 – 2014). The custom SST climatology for the time period and region of this study was built from the NOAA high-resolution (0.25 ° x 0.25°) blended analysis of daily SST data product (OISSTv2,\textsuperscript{48}). The annual climatology presented here is the median and interquartile range of sea surface temperature observations in each of the deployment regions per day of year.

Abbreviations

WBC- West coast of Baja California Peninsula

OAX- Oaxaca

IQR- Interquartile Range

EPO- East Pacific Ocean

WCGPE3- Wildlife Computers Global Position Estimator 3

SST- Sea Surface Temperature

ILD- Isothermal Layer Depth

Declarations

Ethics approval and consent to participate

All organisms were tagged under authority of the Comisión Nacional de Pesca y Acuacultura permit
numbers DAPA/2/130910/044423, DAPA/2/030511/01246, and DGOPA-DAPA-01595/13

**Consent for publication**

“Not Applicable”

**Availability of data and materials**

“The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.”

**Competing interests**

“The authors declare that they have no competing interests”

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**Authors’ contributions**

“SOG, JOS, and RRS conceived and design this research. CRP composed and edited text, managed tags pre deployment and tag data post deployment. SMS analyzed tag data and composed and edited figures, tables and text. WM and MPS composed and edited text. MPS and JD tracked, confirmed and edited references and text, JOS and RR-S tagged all fish, JOS provided funding, RR-S and SOG edited text and provided fisheries expertise. All authors read and approved the final manuscript.”

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References

1. Palko BJ, Beardsley GL, Richards, WJ. Synopsis of the biological data on dolphin-fishes, *Coryphaena hippurus* Linnaeus and *Coryphaena equiselis* Linnaeus. NOAA Tech Rep. 1982; 443.

2. Whoriskey S, Arauz R, Baum, JK. Potential impacts of emerging mahi-mahi fisheries on sea turtle and elasmobranch bycatch species. Biol Conserv. 2011; 144 (6): 1841-1849, http://doi.org/10.1016/j.biocon.2011.03.021.

3. Martínez-Ortiz J, Aires-da-Silva A, Lennert-Cody C, Maunder, M. The Ecuadorian Artisanal Fishery for Large Pelagics: Species Composition and Spatio-Temporal Dynamics. PLOS One. 2015; 10. e0135136. 10.1371/journal.pone.0135136.

4. Merten W, Appeldoorn R, Hammond D. Movements of dolphinfish (*Coryphaena hippurus*) along the U.S. east coast as determined through mark and recapture data. Fish Res. 2014a; 151: 114-121. doi:10.1016/j.fishres.2013.10.021

5. Merten W, Appeldoorn R, Hammond D. Movement dynamics of dolphinfish (*Coryphaena hippurus*) in the northeastern Caribbean Sea: Evidence of seasonal re-entry into domestic and international fisheries throughout the western central Atlantic. Fish Res. 2016; 175: 24-34.

6. IUCN: The IUCN Red List of Threatened Species [Internet]. Version 2017-3 [cited 15 December 2017]. Available from: http://www.iucnredlist.org

7. Fonteneau A, Chassot E, Bodin N. Global spatio-temporal patterns in tropical tuna purse seine fisheries on drifting fish aggregating devices (DFADs): Taking a historical
perspective to inform current challenges. Aquat Living Resour. 2013; 26: 37-48.
doi:10.1051/alr/2013046

8. Magnuson-Stevens Fishery Conservation and Management Act (MSA); Seafood Import Monitoring Program, 50 C.F.R. § 300.324(b)(2) (2016).

9. Aires-da-Silva A, Maunder M. Status of bigeye tuna in the eastern Pacific Ocean in 2012 and outlook for the future. Inter-Amer Trop Tuna Comm Stock Assess Rep. 2014; 14: 31-185.

10. Aires-da-Silva A, Valero JL, Maunder MN, Minte-Vera C, Lennert-Cody C, Román MH, Martínez-Ortiz M, Torrejón-Magallanes EJ, Carranza MN. Exploratory stock assessment of dorado (Coryphaena hippurus) in the southeastern Pacific Ocean. Inter-Amer Trop Tuna Comm Tech doc. SAC-07-06a(i) 2016. [cited March 29, 2018] Available from: http://www.iattc.org/Meetings/Meetings2016/SAC-07/PDFs/Docs/_English/SAC-07-06a(i)-Dorado-assessment.pdf

11. Valero JL, Aires-da-Silva A, Maunder MN, Minte-Vera C, Martínez-Ortiz J, Torrejón-Magallanes EJ, Carranza MN. Exploratory management strategy evaluation (MSE) of Dorado (Coryphaena hippurus) in the south Eastern Pacific Ocean. Inter-Amer Trop Tuna Comm Sci Adv Comm., Seventh Meeting. (2016)

12. Abo-Tubikh NAS. Status and improvement of artisanal fisheries in Manabi province, Ecuador: a case study. Int J Fish Aquat Stud. 2014; 2(2): 47-54

13. Solis PG, Aleman JC, Lujan C, Morales, J. Guia de Buenas Practicas Pesquera. Ministerio de la Produccion Peru. 2015; 1-60.

14. Díaz-Jaimes P, Uribe-Alcocer M, Ortega-Garcia S, Durand JD. Spatial and temporal mitochondrial DNA genetic homogeneity of dolphinfish populations (Coryphaena hippurus) in the eastern central Pacific. Fish Res. 2006; 80(2-3), 333-338. https://doi.10.1016/j.fishres.2006.04.015
15. Díaz-Jaimes P, Uribe-Alcocer M, Rocha-Olivares A, García-de-León FJ, Nortmoon P, Durand JD. Global phylogeography of the dolphinfish (Coryphaena hippurus): the influence of large effective population size and recent dispersal on the divergence of a marine pelagic cosmopolitan species. Mol Phylogenet Evol. 2010; 57: 1209-1218.

16. Oro MG. El Dorado (C. hippurus y C. equiselis) [Internet]. La Pesca Deportiva en México (por la pesca libre y responsable). 1999; [cited 2018]. Available from: http://www.pesca.orgmx/articulos/dorado1.html.

17. Merten W, Appeldoorn R, Rivera R, Hammond D. 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. 2014b; 161: 1823-1834. doi:10.1007/s00227-014-2464-0

18. Whitney NM, Taquet M, Brill RW, Girard C, Schwieterman GD, Dagorn L, Holland KN. Swimming depth of dolphinfish (Coryphaena hippurus) associated and unassociated with fish aggregating devices. Fish Bull. 2016; 114: 426-43

19. Girard C, Dagorn L, Taquet M, Aumeeruddy R, Peignon C, Benhamou S. Homing abilities of dolphinfish (Coryphaena hippurus) displaced from fish aggregating devices (FADs) determined using ultrasonic telemetry. Aquat Living Resourc. 2007; 20: 313-321. doi:10.1051/alr:2008005

20. Dempster T, Taquet M. Fish aggregation device (FAD) research: Gaps in current knowledge and future directions for ecological studies. Rev Fish Bio Fish. 2004; 14: 21-42. doi:10.1007/s11160-004-3151-x

21. Taquet M, Sancho G, Dagorn L, Gaertner J, Itano D, Aumeeruddy R, Peignon C. Characterizing fish communities associated with drifting fish aggregating devices (FADs) in the Western Indian Ocean using underwater visual surveys. Aquat Living Resourc. 2007; 20(4): 331-341. doi:10.1051/alr:2008007
22. Taquet M, Dagorn L, Gaertner JC, Girard C, Aumerruddy R, Sancho G, Itano D. Behavior of dolphinfish (*Coryphaena hippurus*) around drifting FADs as observed from automated acoustic receivers. Aquat Living Resour. 2007; 20: 323–330. doi:10.1051/alr:2008008

23. Martinez-Rincon RO, Ortega-Garcia S, Vaca-Rodriguez JG. Incidental catch of dolphinfish (*Coryphaena* spp.) reported by the Mexican tuna purse seiners in the eastern Pacific Ocean. Fish Res. 2009; 96: 296–302. doi:10.1016/j.fishres.2008.12.008

24. Farrell ER, Boustany AM, Halpin PN, Hammond DL. Dolphinfish (*Coryphaena hippurus*) distribution in relation to biophysical ocean conditions in the northwest Atlantic. Fish Res. 2014; 151: 177–190.

25. Furukawa S, Kawabe R, Ohshimo S, Fujioka K, Nishihara GN, Tsuda Y, Nakata H. Vertical movement of dolphinfish, *Coryphaena hippurus*, as recorded by acceleration data-loggers in the northern East China Sea. Environ Bio Fishes. 2011; 92(1): 89-99. doi: 10.1007/s10641-011-9818-y

26. Hernández-Tlapale C, Ketchum JT, Marín-Enríquez E, Muhlia-Melo A. Horizontal and vertical movements of the common dolphinfish (*Coryphaena hippurus*) in La Paz Bay, Mexico. Cienc Mar. 2015; 41(4) doi: 10.7773/cm.v41i4.2560

27. Lin SJ, Musyl MK, Wang SP, Su NJ, Chiang WC, Lu CP, Tonoe K, Wu CY, Sasaki A, Nakamura I, Komeyama K, Kawabe R. Movement behavior of released wild and farm-raised dolphinfish *Coryphaena hippurus* tracked by pop-up satellite archival tags. Fish Sci. 2019; 85: 779 https://doi.org/10.1007/s12562-019-1334-y

28. PRODUCE. 2016. Plan de Acción Nacional para la Conservación y Manejo del recurso Perico en el Perú (PAN-Perico), Resolución Viceministerial N°81.2016.PRODUCE/DVPA, Lima, Perú
29. Zúñiga Flores MS, Ortega-García S, Klett-Traulsen A. Interannual and seasonal variation of dolphinfish (*Coryphaena hippurus*) catch rates in the southern Gulf of California, Mexico. Fish Res. 2008; 13-17. Doi: 10.1016/j.fishres.2008.06.003

30. Hammann MG, Palleiro-Nayar JS, Sosa-Nishizaki, O. (1995). The effects of the 1992 El Niño on the fisheries of Baja California, Mexico. Cal Coop Ocean Fish. 1995; 36: 127-133.

31. Norton JG, Crooke SJ. Occasional availability of dolphin, *Coryphaena hippurus*, to southern California commercial passenger fishing vessel anglers: Observations and hypotheses. Cal Coop Ocean Fish. 1994; 35: 230-239.

32. Norton JG. Apparent habitat extensions of dolphinfish (*Coryphaena hippurus*) in response to climate transients in the California Current. Sci Mar. 1999; 63 (3-4): 239-260. http://doi.org/10.3989/scimar.1999.63n3-4261

33. Alejo-Plata C, Díaz-Jaimes P, Salgado-Ugarte IH. Sex ratios, size at sexual maturity, and spawning seasonality of dolphinfish (*Coryphaena hippurus*) captured in the Gulf of Tehuantepec, Mexico. Fish Res. 2001; 110: 207-216. doi: 10.1016/j.fishres.2011.04.008

34. Oxenford H, Hunte W. Feeding habits of the dolphinfish (*Coryphaena hippurus*) in the eastern Caribbean. Sci Mar. 1999; 63: 303-315.

35. Hemphill H. Conservation on the high seas—drift algae habitat as an open ocean cornerstone. Parks. 2005; 15 (3): 48-56

36. 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. Vertical movements of Pacific bluefin tuna (*Thunnus orientalis*) and dolphinfish (*Coryphaena hippurus*) relative to the thermocline in the northern East China Sea. Fish Res. 2014; 14: 86-91.
37. Marín-Enríquez E, Seoane J, Muhlia-Melo A. Environmental modeling of occurrence of
dolphinfish (Coryphaena spp.) in the Pacific Ocean off Mexico reveals seasonality in
abundance, hot spots and migration patterns. Fish Oceanog. 2018; 27: 28–40. doi:
10.1111/fog.12231

38. Yoshida-Hernández H. Variabilidad ambiental y su efecto en la distribución
espacio-temporal de las tasas de captura de dorado (coryphaena hippurus) en la
región de los Cabos B.C.S., México [thesis], Ciencias Marinas del Instituto Politécnico
Nacional, La Paz, Mexico. 2015

39. Santana-Henández H, Ortega-Garcia S, Valdez-Flores JV. Variación espacio-temporal
de las capturas incidentales de dorado (Coryphaena hippurus) en el Pacífico Central
mexicano. El Vigia. 2011; 16 (39).

40. Braun CD, Galuardi B, Thorrold SR. HMMoce: An R package for improved geolocation
of archival-tagged fishes using a hidden Markov method. Methods Ecol Evol. 2018;
9(5):1212–20. doi: 10.1111/2041-210X.12959.

41. Thys TM, Ryan JP, Dewar H, Perle CR, Lyons K, O'Sullivan J, Farwell C, Howard MJ,
Weng KC, Lavaniegos BE, Gaxiola-Castro G, Miranda-Bojorquez LE, Hazen EL, Bograd
SJ. Ecology of the Ocean Sunfish, Mola mola, in the southern California Current
System. J Exp Mar Biol and Ecol. 2015; 471: 64-76. doi: 10.1016/j.jembe.2015.05.005

42. Basson M, Bravington MV, Hartog JR, Patterson TA. Experimentally derived likelihoods
for light-based geolocation. Methods Ecol and Evol. 2016; 7(8):980-9.

43. Perle CR. Transpacific migrations of Pacific bluefin tuna. In: Movements and
migrations of manta rays, pacific bluefin tuna, and white sharks: observations and
insights at the intersection of life history strategy and marine ecosystem structure
[dissertation]. Palo Alto, CA, Stanford University. 2011.

44. Wildlife Computers.2018. Location Processing (GPE3 & Fastloc) in the Wildlife
Computers Data Portal User Guide.

https://static.wildlifecomputers.com/manuals/Location-Processing-User-Guide.pdf

Accessed May 17, 2019

45. Mager EM, Esbaugh AJ, Stieglitz JD, Hoenig R, Bodinier C, Incardona JP, Scholz NL, Benetti DD, Grosell M. Acute Embryonic or Juvenile Exposure to Deepwater Horizon Crude Oil Impairs the Swimming Performance of Mahi-Mahi (*Coryphaena hippurus*) Environ Sci Technol. 2014; 48(12):7053-61

46. Stieglitz JD, Mager EM, Hoenig R, Benetti DD, Grosell, M. Impacts of Deepwater Horizon Crude Oil Exposure on Adult Mahi-Mahi (*Coryphaena hippurus*) Swim Performance. Environ Toxicol. 2016; 35(10):2613-2622. doi: 10.1002/etc.3436.

47. Kara AB, Rochford PA, Hurlburt HE. An optimal definition for ocean mixed layer depth. J Geophys Res. 2010; 105 (C7):16,803 – 16,821.

48. Reynolds RW, Smith TM, Liu C, Chelton DB, Casey KS, Schlax MG. Daily High-Resolution-Blended Analyses for Sea Surface Temperature. J Clim. 2007; 20: 5473-5496.

Figures
Tag deployment locations. Dashed line boxes indicates extent of west coast of Baja California Peninsula (WBC) and Oaxaca (OAX), Mexico. White circles represent approximate tagging locations with a trip number. Trip information associated with these numbers is available in Table 1.
Example of model run selection for fish 111522. Multiple iterations of the WC-GPE3 were run per fish to select an optimal value of animal speed for the model input. The trade-off between model optimization (cut-off represented by dashed line) and the size of the area of uncertainty is shown in the main graphic with the color representing the animal speed input parameter for that model run. The inset shows a subset of the potential tracks using the same color-code. The black markers denote the model parameter and track used in the final analysis.
Figure 3

Size Distributions of (A) all tagged fish and (B) those outfitted with electronic tags. (*) indicates significant difference (p < 0.05) within region between fish deployed and (A) recovered or (B) reported electronically while (**) indicates significant difference (p < 0.05) across regions.
Figure 4

Horizontal movement of tagged dolphinfish. Deployment (circles) and recovery (squares) locations are color coded according to year. Dashed lines denote conventional tag displacements. Solid lines denote displacement from deployment to electronic tag reporting location. Daily locations estimated by WC-GPE3 are represented by smaller markers, 95% likelihood areas surrounding each position estimate are colored by season. Small marker type denotes sex (females = circles; males = squares).
Home range extents in (A) latitude and (B) longitude as a function of time at liberty. Sex is denoted by shape (circles = female; squares = male), and region is denoted by color. Filled markers represent electronic tag displacements, open markers are conventional tag data.

Figure 5
Examples of differences in types of diurnal diving behaviors. The black circles and lines represent the fish depth over time and gray bars denote nighttime. In panel A, daytime depths are deeper than nighttime depths, typical of diel vertical migration of prey; in panel B, the pattern is reversed.
Regional patterns in (A) sea surface temperature and (B) depth of the isothermal layer depth (ILD) experienced by WBC (black) and OAX (blue) tags. In (A), thick lines represent the median sea surface temperature and are bounded by lower and upper values representing the 25 and 75 percentiles. Observed SST values from electronic tags are filled circles. Arrows denote temporal range of the tagging dataset for each region. In (B), filled bars represent the frequency of ILD binned in 10 meter increments - the dashed lines represent the median ILD for each region as determined by tag data.
Figure 8

Thermal habitat experienced by tagged fish with distributions of (a) median daily temperature, (b) minimum daily temperature, and (c) proportion of time spent in top 5 m versus sea surface temperature. In panels (a) and (b), each dot represents one day of data in either the WBC (black) or OAX (blue) region and the dashed lines represent the best-fit trendline of the regression for both regions. In panel (c), the dots represent the median while the lines represent the 25th and 75th percentiles of percent time in the top 5 m per day within 1°C SST bins.

Supplementary Files
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