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Influence of temperature and oxygen on the distribution of blue marlin (*Makaira nigricans*) in the Central Pacific

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ABSTRACT

The blue marlin (*Makaira nigricans*) is a highly migratory pelagic predator of tropical and subtropical seas. Information on the habitat use of marine species is fundamental to understanding their ecology and population dynamics and is needed to inform responsible management strategies. Using a long-term satellite tagging data set from The International Game Fish Association Great Marlin Race, we examined habitat use and how oxygen and temperature influence the horizontal and vertical distributions of blue marlin in the Central Pacific. Blue marlin primarily occurred in warm waters (26–30°C) and exhibited a diel bimodal depth distribution across the 5-year data record (2009–2013), with fish spending the majority of their time near the surface at night and at deeper depths during the day (25–100 m). The depth distribution of blue marlin was limited in areas where low oxygen and/or temperature conditions occur closer to the surface, with the extent of habitat compression being greatest when both oxygen and temperature were limiting. The migrations of blue marlin appeared restricted during the 2010 La Niña, when increased equatorial upwelling resulted in an extension of the cold, low oxygen waters of the cold tongue into the Central Pacific, creating a barrier to the trans-equatorial migrations that occurred during all other tagging years. If the frequency and intensity of La Niña events increases and the oxygen minimum layer continues to expand as has been predicted under certain climate change scenarios, the migratory behavior and habitat availability of blue marlin may be impacted.

Key words: billfish, El Niño Southern Oscillation, habitat compression, migration, oxycline, satellite tag

INTRODUCTION

Understanding the movements of pelagic fish and the influence that environmental conditions have on their vertical and geographic distribution is fundamental to understanding their ecology and necessary for effective management (Brill and Lutcavage, 2001; Bigelow and Maunder, 2007). Patterns of movement and habitat use directly influence the susceptibility of a species to fisheries. Hence, understanding the environmental drivers that influence the movements and habitat use of a species allows researchers to model and predict where and when a species will be vulnerable to fishing pressure, which is critical for effective management (Brill and Lutcavage, 2001). However, determining these relationships in pelagic species has been very difficult because of their migratory habits, large size, and the remote nature and apparent homogeneity of their oceanic habitats. The distribution and migratory patterns of pelagic fish have historically been studied using fisheries catch data and tag-recapture data yet these approaches often lack the resolution necessary to characterize habitat use and environmental preferences on a biologically relevant spatial and temporal scale (Brill and Lutcavage, 2001; Kohler and Turner, 2001; Fonteneau and Richard, 2003). Electronic tags have provided researchers with a powerful tool to study the biology of these difficult to study animals, and have provided great insight into the habitat use and environmental preferences of a variety of pelagic organisms (Shaffer *et al.*, 2006; Shillinger *et al.*, 2008; Block *et al.*, 2011).

Blue marlin (*Makaira nigricans*) are large, oceanic predators that are circumglobally distributed across

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tropical and subtropical waters (Finnerty and Block, 1992; Graves and McDowell, 1995). They are primarily epipelagic, remaining in the mixed layer, but they are capable of diving to depths in excess of 800 m (Goodyear *et al.*, 2008). The majority of satellite tag studies of blue marlin have occurred in the Atlantic and the Gulf of Mexico, and have demonstrated that blue marlin exhibit a bimodal depth distribution, spending most of their time near the surface (<5–10 m) at night and diving to greater depths (~40–100 m) during the day (Goodyear *et al.*, 2008; Kraus *et al.*, 2011). Short-term acoustic tracks, lasting hours to days, suggest a similar pattern in the waters around Hawaii (Holland *et al.*, 1990; Block *et al.*, 1992a). Throughout their range, they primarily occur in sea surface temperatures (SST) above 24°C although they usually occur in warmer waters from 26 to 30°C (Holland *et al.*, 1990; Graves *et al.*, 2001; Goodyear *et al.*, 2008). SST changes related to the El Niño Southern Oscillation cycle (ENSO) have been shown to influence the geographic distributions of blue marlin, with their distribution shifting east as water temperature warmed and mixed layer depths increased (Su *et al.*, 2011a). The vertical distribution of blue marlin and other pelagic fish is also influenced by the thermal structure of the water column in addition to low oxygen conditions (Green, 1967; Brill *et al.*, 1999; Prince and Goodyear, 2006). Intense upwelling brings low oxygen and low-temperature waters close to the surface in the Eastern Tropical Pacific (ETP) and Atlantic (ETA), which results in a compression of vertical habitat for blue marlin and other pelagic fishes (Prince and Goodyear, 2006; Prince *et al.*, 2010; Stramma *et al.*, 2012). This may be of particular importance as climate change is driving an expansion and shoaling of the oxygen minimum zones (OMZ) in the ETP and ETA, with potentially important ecological and ecosystem effects, including loss of habitat for tropical pelagic fishes (Stramma *et al.*, 2008).

The relative importance of temperature and oxygen in determining the vertical distribution of blue marlin remains unclear. In areas of the ETP and ETA, where vertical habitat compression in blue marlin has previously been described (Prince and Goodyear, 2006), there is consistent strong upwelling and blue marlin encounter steep gradients in temperature and oxygen at shallow depths, thereby being subjected to thermal and oxygen limitations at the same time (Prince *et al.*, 2010). Whether vertical habitat compression is more influenced by oxygen or thermal condition, or whether there are additive physiological effects of both oxygen and temperature limitation, remains unclear. If we are to understand and predict how blue marlin will respond to an expansion of the OMZ and changing thermal structure of the water column in the future with climate change (Ekau *et al.*, 2010; Gilly *et al.*, 2013), we need to understand their habitat use and elucidate the role that temperature and oxygen play in influencing their horizontal and vertical distribution.

Detailed information on habitat use is needed to understand the ecology of this species and foster effective management as blue marlin are one of the most important bycatch species in pelagic fisheries in the Pacific (Molony, 2005), and they have been listed as vulnerable by the International Union for Conservation of Nature (Collette *et al.*, 2011). Habitat availability of blue marlin likely changes over a variety of spatial and temporal scales as the equatorial Pacific experiences dynamic seasonal changes in SST and water column thermal and oxygen structure related to equatorial upwelling. Additionally, large-scale changes in oceanographic conditions, such as those driven by ENSO, also likely influence the availability of habitat for blue marlin (Wyrtki, 1975; Wyrtki and Eldin, 1982; Su *et al.*, 2008). In this paper, we utilize a unique, multi-year satellite tag dataset for blue marlin tagged in the Central Pacific as part of the IGFA Great Marlin Race (IGMR) to (i) investigate inter-annual patterns of movement and habitat use of blue marlin in the Central Pacific and (ii) elucidate the role that temperature and oxygen play in determining the horizontal and vertical distribution of blue marlin, particularly in response to equatorial upwelling and the ENSO cycle.

MATERIALS AND METHODS

The data used in this study were primarily obtained through a collaboration between scientists at Stanford University, the International Game Fish Association, and captains, crews, and anglers participating in the Hawaiian International Billfish Tournament (HIBT). In recognition of the key role this tournament has played in the history of electronic tag development (the first prototype pop-up satellite tags were tested at the HIBT in the mid-1990's), anglers at the 50th HIBT tournament in 2009 were offered the opportunity to sponsor and deploy electronic tags on Pacific blue marlin they caught and released – with the blue marlin traveling the greatest distance being declared the winner of the 'Great Marlin Race'. The initial effort was so successful that it became an annual part of the HIBT, engaging anglers from around the world to participate directly in the research program. This program gave rise to the larger IGFA Great Marlin Race tagging program (https://igmr.igfa.org/Conserve/IGMR.aspx).

Study Location

Blue marlin were tagged off the west coast of Hawaii in July–September of each year from 2009 to 2013, in association with the annual HIBT at Kailua-Kona. In the South Pacific, tags were deployed off the island of Tahiti in French Polynesia in February–April of 2013 (Table 1).

Tagging methods

Blue marlin were tagged with pop-up archival transmitting tags (PAT) from Wildlife Computers (Redmond, WA, USA). In the Hawaii deployments from 2009–2012, MK10 PAT tags were used; in 2013 Mini-PAT tags were used both in Hawaii and in Tahiti. Tags recorded temperature, pressure, and light data which were summarized into 24-h histogram bins for transmission to the Argos satellite system. Temperature bins were 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30 and >30°C. Depth bins were −1, 5, 10, 25, 50, 100, 150, 200, 250, 300, 500, 1000 and >1000 m. The binning structure for miniPATs was changed in 2013 to better reflect the distribution of blue marlin. The updated bin structure for temperature was 18, 20, 22, 23, 24, 25, 26, 27, 28, 29, 30 and >30°C. The updated depth bins were 5, 10, 25, 50, 75, 100, 125, 150, 200, 250, 300 and >300 m. Tags were programmed to release after 120, 180 or 240 days (Table 1). Tags were painted with black anti-fouling paint (Trilux 33; International Paint LLC, Union, NJ, USA) and leadered with 136 kg (300 lbs) monofilament fishing line (Moi-Moi 'marlin' ultra hard), shrouded in braided aramide and encased in two layers of heat shrink wrap to protect from abrasion. The leader was affixed to the tag at one end and a 6 × 1.3-cm titanium anchor at the other using stainless steel crimps, such that the overall leader length from the tag to the anchor was approximately 16.5 cm.

Blue marlin were caught on rod and reel with artificial baits, trolled in spreads of four or five lures off sport fishing vessels at 7–10 knots (1 knot = 1.852 km h^{-1}). Once a blue marlin was caught on hook and line, the fish was leadered close to the fishing vessel and brought alongside the boat, at which time a 2-m tagging pole fitted with a 15-cm applicator tip was used to insert the titanium anchor into the dorsal musculature of the blue marlin just below the leading edge of the dorsal fin. Once the tag was affixed, the hook was removed from the blue marlin's mouth and the fish released. Weights were estimated during tagging. All deployment metadata, including time, date, location, size, etc., were recorded immediately after release.

Analysis

Data transmitted by PAT tags were processed using the Wildlife Computers software (DAP Processor; Wildlife Computers, Redmond, WA, USA) providing daily summaries of binned time-at-depth (TAD), binned time-at-temperature (TAT), PDTs (temperature depth profiles), and light levels. Daily geolocation estimates were generated using the method described by Teo *et al.* (2004) and tracks further processed using a Bayesian state-space model as described in Block *et al.* (2011) and Winship *et al.* (2012).

Binned TAD and TAT data were analyzed to investigate the vertical and thermal distribution of blue marlin in the Central Pacific. The mean (±SD) proportion of time spent in each depth and temperature bin was calculated for each year and tagging location (HIBT 2009–2013; Tahiti, 2013). For each day of data, we estimated four additional depth metrics, the 95%, 90%, 75%, and 50% depths, which represent an estimate of the depth above which blue marlin spent a given proportion of their day assuming that the blue marlin were uniformly distributed within each depth bin. Based on this assumption of their distribution within bins, we interpolated across the binned depth data to reconstruct a continuous depth distribution and estimate the cumulative proportion of time spent above each meter of their full depth range, with the maximum depth set by the daily maximum depth recorded by the tag (Supporting Information Fig. S1).

To investigate the thermal and dissolved oxygen (DO) structure of the water columns used by blue marlin, we used daily *in-situ* temperature and depth data recorded by the tags to recreate daily temperature-depth profiles based on the transmitted PDT datasets and monthly climatological dissolved oxygen data from the World Ocean Atlas (WOA) to generate daily oxygen-depth profiles. PDTs summarize all of the daily temperature and depth data recorded by the tag into the minimum, mean, and maximum temperatures that occur at eight depths over the course of each day, ranging from the shallowest to deepest depth and at six equal intervals between these depths. We interpolated across these eight depths using piecewise cubic hermite interpolation to create the daily temperature-depth profile. We used the reconstructed temperature-depth profile to estimate isothermal layer depth, a proxy for mixed layer depth, based on Kara *et al.* (2000). We extracted maximum daily depths and daily

Table 1. Blue marlin tagged in Hawaii at the Hawaiian International Billfish Tournament (HIBT) and in French Polynesia. Prog. length is programmed deployment duration, DAL is days at liberty (track duration). Pop-up distance is the distance between tagging and pop-up location. Total distance is the cumulative distance of the track. Weights were estimated at the boat and used to estimate FL (see Materials and Methods). Minimum and maximum temperatures are the most extreme temperatures encountered by the marlin over the course of its track.

ID	Year	Location	Tag type	Prog length (days)	Tag date	Pop-up date	DAL	Pop-up distance (km)	Total distance (km)	Max depth (m)	Max temp (°C)	Min temp (°C)	Wt (kg)	FL (cm)
5509003	2009	Hawaii	MK10	180	7/22/09	10/23/2009	94	4121	5511	232	30.2	15.6	64	224
5509007	2009	Hawaii	MK10	180	7/24/09	8/1/2009	9	115	222	176	27.4	17.6	N/A	N/A
5509008	2009	Hawaii	MK10	180	8/3/09	1/26/2010	177	1919	4991	280	27.8	10.2	113	272
5509009	2009	Hawaii	MK10	180	8/4/09	1/30/2010	180	4910	8002	240	30.4	13.4	82	244
5509010	2009	Hawaii	MK10	180	8/7/09	11/4/2009	90	3421	4728	376	29.6	9.6	113	272
5510001	2010	Hawaii	MK10	120	8/3/10	12/1/2010	120	4226	6454	184	28.4	13.4	68	230
5510002	2010	Hawaii	MK10	120	8/3/10	10/7/2010	66	2524	2997	240	30.4	11.2	82	244
5510003	2010	Hawaii	MK10	120	8/4/10	9/10/2010	37	1280	1276	216	28	13	77	239
5510004	2010	Hawaii	MK10	120	8/9/10	9/24/2010	46	1435	1566	168	27.8	13.6	79	242
5510005	2010	Hawaii	MK10	120	8/10/10	11/6/2010	88	1846	3517	200	29.8	13	77	239
5510006	2010	Hawaii	MK10	120	8/11/10	9/8/2010	29	926	1181	232	27.4	11	68	230
5510008	2010	Hawaii	MK10	120	8/11/10	12/10/2010	121	189	1275	256	27.8	15	102	263
5510009	2010	Hawaii	MK10	120	8/16/10	12/14/2010	120	1661	5713	200	28.8	13.2	45	201
5510010	2010	Hawaii	MK10	120	8/16/10	9/18/2010	33	157	479	280	27.6	14	68	230
5511004	2011	Hawaii	MK10	120	7/28/11	9/4/2011	38	954	1614	200	28.2	11	91	253
5511006	2011	Hawaii	MK10	120	7/29/11	10/5/2011	67	1904	1377	152	28.6	16.4	41	194
5511007	2011	Hawaii	MK10	120	7/29/11	9/26/2011	58	1950	5809	168	29.2	14.4	91	253
5511009	2011	Hawaii	MK10	120	8/2/11	11/30/2011	120	3245	8022	368	28	12.2	136	289
5511010	2011	Hawaii	MK10	120	8/3/11	12/2/2011	121	4052	19485	256	28.2	10	77	239
5511012	2011	Hawaii	MK10	120	8/28/11	11/9/2011	73	967	7731	248	26.8	11.4	82	244
5512014	2012	Hawaii	MK10	180	8/13/12	11/12/2012	91	2219	3962	208	28.8	15.2	136	289
5512016	2012	Hawaii	MK10	180	8/13/12	11/8/2012	88	3228	4505	208	29	12	82	244
5512017	2012	Hawaii	MK10	180	8/14/12	9/19/2012	36	1835	2118	176	29.2	12.2	91	253
5512018	2012	Hawaii	MK10	180	8/14/12	10/1/2012	48	1971	2603	200	28.4	12.4	91	253
5512019	2012	Hawaii	MK10	180	8/14/12	10/16/2012	64	1220	1180	168	27.8	18.8	68	230
5512020	2012	Hawaii	MK10	180	8/16/12	10/22/2012	66	261	1734	192	28.6	18.4	59	219
5512021	2012	Hawaii	MK10	180	8/17/12	10/17/2012	61	280	719	272	28.6	15	54	213
5512022	2012	Hawaii	MK10	180	8/21/12	9/25/2012	36	656	1646	128	26.8	21.2	113	272
5512023	2012	Hawaii	MK10	180	9/6/12	1/2/2013	118	945	3739	416	27	9.2	91	253
5513001	2013	Fr. Poly.	miniPAT	240	2/21/13	10/19/2013	241	3011	11167	360	30.6	9.2	68	230
5513002	2013	Fr. Poly.	miniPAT	180	2/21/13	8/21/2013	5	406	407	160	29.4	23.2	75	237
5513003	2013	Fr. Poly.	miniPAT	180	3/10/13	9/6/2013	181	333	4534	504	29.8	8.8	68	230
5513005	2013	Fr. Poly.	miniPAT	180	3/23/13	5/21/2013	59	622	1800	320	30.4	15.8	45	201

Table 1. (*Continued*)

ID	Year	Location	Tag type	Prog length (days)	Tag date	Pop-up date	DAL	Pop-up distance (km)	Total distance (km)	Max depth (m)	Max temp (°C)	Min temp (°C)	Wt (kg)	FL (cm)
5513007	2013	Fr. Poly.	miniPAT	240	3/30/13	11/25/2013	241	1319	2715	408	30.4	9.4	45	201
5513010	2013	Fr. Poly.	miniPAT	240	4/7/13	10/23/2013	200	30	1596	504	29.4	7.8	215	336
5513011	2013	Fr. Poly.	miniPAT	240	4/12/13	12/10/2013	243	3363	11654	416	30.2	9	54	213
5513020	2013	Hawaii	miniPAT	180	8/9/13	2/5/2014	181	5339	12594	616	29.2	6.4	113	272
5513021	2013	Hawaii	miniPAT	180	8/20/13	12/12/2013	115	2135	3591	672	27.4	5.4	318	382
5513023	2013	Hawaii	miniPAT	180	9/5/13	2/27/2014	175	3891	8625	712	30	5.8	57	216
5513024	2013	Hawaii	miniPAT	180	9/13/13	3/12/2014	181	137	2142	520	28	6.4	145	295
5513025	2013	Hawaii	miniPAT	180	9/16/13	3/16/2014	181	244	4568	472	28.6	8	82	244

mean SST and minimum temperatures from the PDT files as well.

To estimate the dissolved oxygen environment the blue marlin may have experienced, we extracted climatological dissolved oxygen data for the appropriate location and month from the World Ocean Atlas 2013 (Garcia *et al.*, 2014) to generate an oxygen-depth profile for each position. We binned the interpolated TAD distribution (see Materials and Methods, Supporting Information Fig. S1) into the depth bins that correspond with the WOA oxygen depth bins and used the rebinned TAD data to estimate time spent at different oxygen levels (TAO). Note that because daily temperature-depth profiles were based on *in-situ* data and oxygen-depth profiles were based on monthly climatological data, temperature data accurately reflect the thermal environment blue marlin encountered, whereas the oxygen data represents the long-term average for a given location and month, leading to some mismatch between the blue marlin behavior and dissolved oxygen data since *in-situ* dissolved oxygen levels vary from the climatological mean from year to year. Despite this limitation, patterns in spatial and temporal variability in dissolved oxygen from WOA climatological DO data provide a good general representation of the broad-scale trends in dissolved oxygen that the blue marlin would experience while moving across the Central Pacific.

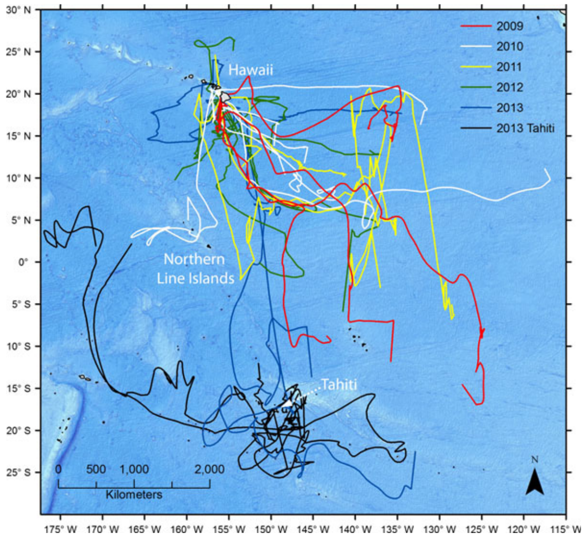
We used the daily temperature and monthly oxygen-depth profiles to estimate the minimum temperatures and oxygen levels that blue marlin encountered. To estimate the minimum temperature at depth encountered by blue marlin for each day of data, we used the minimum temperature recorded at the maximum depth from the PDT file. To estimate the minimum dissolved oxygen encountered by blue marlin, we used the minimum dissolved oxygen level predicted to occur at their maximum depth from the oxygen-depth profile for that location and month. We then calculated the average minimum temperature and dissolved oxygen levels encountered by blue marlin and used these values and the temperature and oxygen-depth profiles to estimate the depth at which these values occurred for each day of data. We used these minimum temperature and dissolved oxygen levels to set a reasonable lower threshold for the thermal and dissolved oxygen habitat for blue marlin from this study.

We then calculated the median depth at which these minimum dissolved oxygen and temperature levels occurred across the entire dataset. These median depths were used to group each day into one of four habitat categories based on whether the depth of the minimum oxygen and temperature levels were shallower or deeper than the median depths for each parameter (Supporting Information Fig. S3). The depths at which these environmental conditions occurred were used as a metric for potential vertical habitat compression. Based on this, each day was categorized as being not limited (N, oxygen and temperature should not be limiting), oxygen limited (O, oxygen may be limiting), temperature limited (T, temperature may be limiting) or oxygen and temperature limited (OT, both temperature and oxygen may be limiting). If a fish had less than 3 days in a habitat group, we discarded those days from that habitat group's dataset. We then calculated the median maximum depth, 95% depth, 90% depth, 75% depth, and 50% depth for each of these groups. We then tested whether median values for each depth metric varied across each habitat group for all the fish using either a one-way ANOVA or a Kruskal–Wallis One-Way Analysis of Variance on Ranks using Dunn's Method for pairwise multiple comparison tests in situations where data did not meet the assumptions of normality and homogeneity of variances. All statistics were conducted in SIGMAPLOT 12 (Systat Software Inc., San Jose, CA, USA).

RESULTS

Between 2009 and 2013, a total of 59 blue marlin were tagged in Hawaii and Tahiti, with the majority being tagged off the coast of Kona, Hawaii (n = 47) and the remainder being tagged in Tahiti (n = 12) in 2013. Out of these tags, a total of 18 (30%) did not report data, and in this paper we use data from the 41 tags that did report (Table 1). The estimated average weight of the tagged blue marlin was 90.7 kg (±48.7 SD), which based on the length-weight relationship from Skillman and Yong (1974) converts to a mean fork length (tip of the snout to fork of the tail) of 247.0 cm (±35.7). Cumulatively, there were 3639 days of tracking data, with an average tag deployment of 104.8 days (±65.4). Over the course of the deployments, the average minimum distance moved (the distance from tagging to pop-up location) was 1835.3 km (±1450.3) whereas average length of reconstructed tracks was 4379.2 km (±3935.6). Overall, fish tagged in Hawaii generally moved in a southeasterly direction, with virtually no movements to the north or west (Fig. 1). Fish tagged in Tahiti generally remained within the region, although the two fish that moved the greatest distance both moved along a similar trajectory to the northwest, ending up in an area to the west of the northern Line Islands.

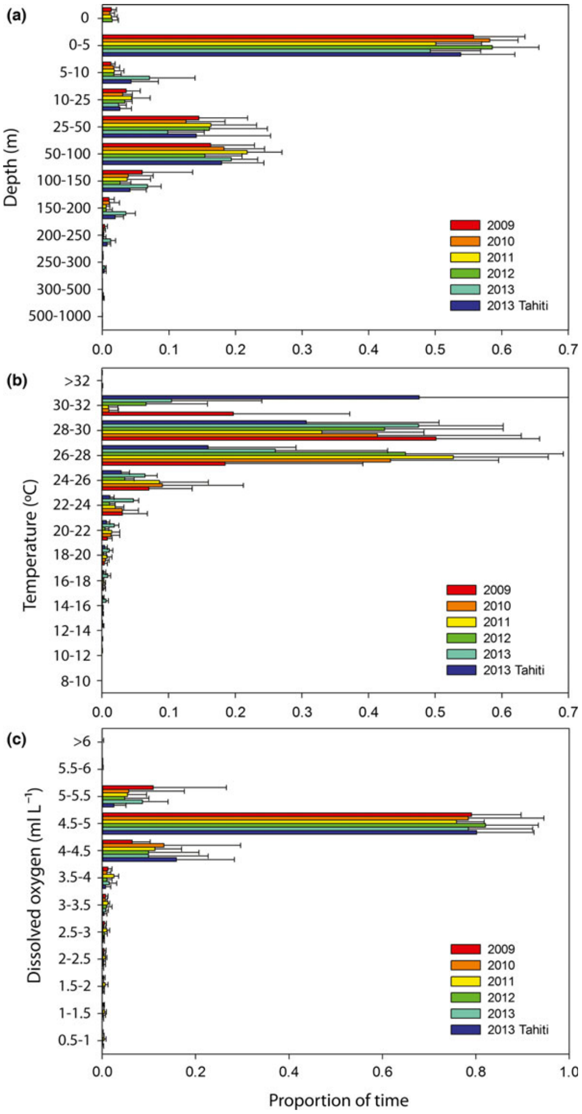
Figure 1. Tracks from blue marlin (n = 41) tagged in the Central Pacific between 2009 and 2013. All tagging occurred off Kailua-Kona, Hawaii except for tags deployed in Tahiti in 2013.



Across all years and regions, blue marlin exhibited a remarkably consistent bimodal depth distribution where they spent the majority of their time at shallow depths (<5–10 m) and at deeper depths between 25 and 100 m (Fig. 2a). Overall, blue marlin rarely dove below 200 m and spent the majority of their time within the isothermal layer (Table 2).

This epipelagic distribution of blue marlin is reflected in their preferences for warm thermal habitats. Blue marlin spent most of their time (>90%) at temperatures between 24 and 30°C (Fig. 2b) and SSTs between 25 and 29°C (mean 26.90 ± 1.37, Fig. 3). Blue marlin tagged in Tahiti had the highest use of warmer temperatures, spending the most time in 28–30°C water (Fig. 2b). This reflects the warmer temperature of the mixed layer around French Polynesia relative to Hawaii as opposed to differences in depth distribution, as these fish exhibited the same time-at-depth profile as all of the other fish tagged (Fig. 2a). Fish tagged in 2009 also spent more time in the warmest temperature bin (28–30°C), which reflects the warm El Niño conditions of that year, while those tagged in 2010 spent more time in cooler temperatures, reflecting the cooler La Niña conditions (http://www.esrl.noaa.gov/psd/enso/mei/) (Fig. 2b). The deepest depth profiles and coldest temperatures recorded both occurred in fish tagged in 2013. The maximum dive depth occurred in fish 5513023, which dove to a depth of 712 m and encountered temperatures of 5.8°C at approximately –149.36°W 11.68°N.

Figure 2. Yearly plots of time at depth (TAD, a), time at temperature (TAT, b), and time at oxygen (TAO, c) for blue marlin tagged in Hawaii (n = 34) and French Polynesia (n = 7). Note that in 2013, miniPATs were used, which had one less bin than the MK10s used in previous years, and as a result did not have the shallowest and coldest bin.

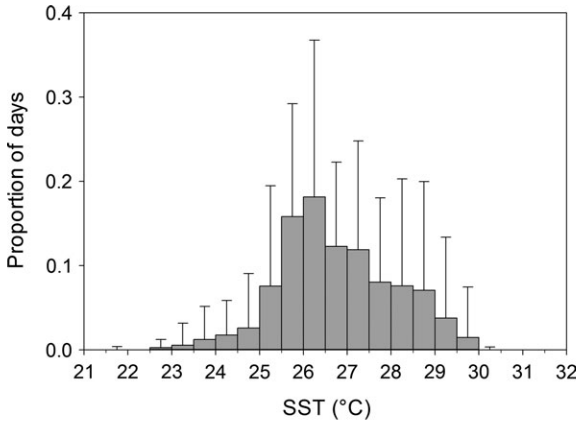


The coldest temperature was encountered by the largest blue marlin tagged (5513021) which encountered a temperature of 5.4°C at a depth of 672 m at approximately –153.42°W 17.84°N. Based on estimates from WOA climatological data, blue marlin almost always occurred at dissolved oxygen levels above 4.0 mL L^{-1}, and spent ~80% of their time in regions of the water column with oxygen levels between 4.5 and 5.0 mL L^{-1} (mean of individuals 4.7 mL L^{-1} ± 0.21 SD, Fig. 2c).

Table 2. Additional depth metrics for blue marlin tagged in this study. Depths are the mean (±SD) depths (meters) above which marlin spent 50, 75, 90, and 95% of their time, as well as the maximum depth. *ILD is time (daily mean %) blue marlin spent within the isothermal layer, a proxy for mixed layer depth.

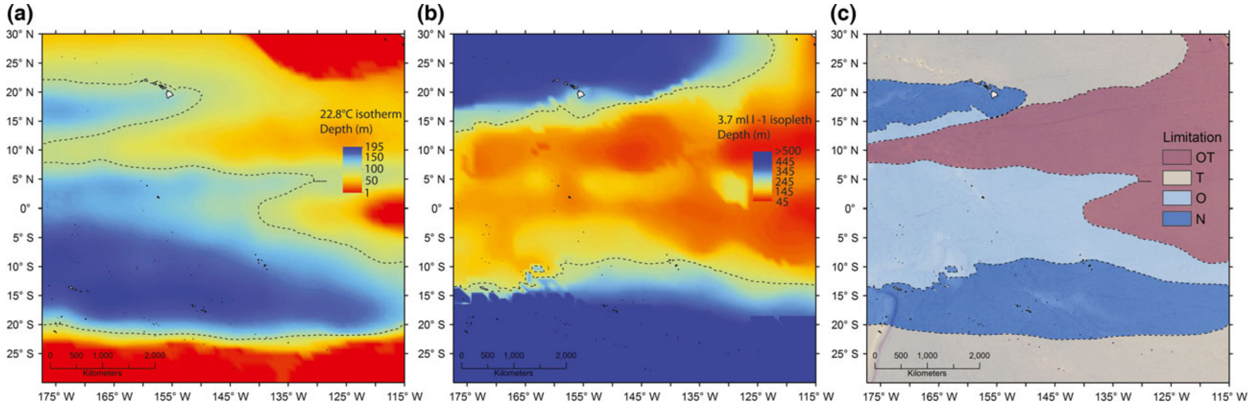
Depths	Mean depth (m)	SD
50%	12.0	13.9
75%	50.4	30.3
90%	84.4	41.1
95%	104.6	47.2
Maximum	164.8	76.4
ILD*	64.9	23.5

Figure 3. The mean sea surface temperature (±SD) experienced by blue marlin tagged in the Central Pacific.



The average minimum temperature (minimum temperature at the deepest depth) experienced by blue marlin was 18.2°C (±4.6). We used the average + 1 SD minimum temperature (22.8°C) as a conservative estimate of minimum temperature. Based on WOA oxygen-depth data, the average minimum oxygen level encountered by blue marlin (oxygen level at deepest depth) was 3.7 mL L^{-1}. The median depth at which the 3.7 mL L^{-1} isopleth occurred was 207 m, whereas the median depth at which the 22.8°C isotherm occurred was 103 m (Supporting Information Fig. S3). The depths at which these threshold values occurred were dynamic and changed over time and space (Fig. 4). Based on these threshold values, ~30% of the data set, representing 25 fish, were assigned to the no temperature or oxygen limitations group (Group N), ~17% of the data, representing 16 fish, were assigned to the temperature limited group (Group T), ~19% of the data, representing 25 fish, were assigned to the potentially oxygen limited group (Group O), and

Figure 4. An example of the spatial variability in the depth of the 22.8°C isotherm (a, dashed line) and 3.7 mL L^{-1} dissolved oxygen isopleth (b, dashed line) during October based on data from the World Ocean Atlas (WOA). When the depth of the isotherm/isopleth is shallower than the median depth for that variable (103 m for temperature, 207 m for oxygen), temperature or oxygen were considered to be potentially limiting. (c) shows habitat groupings based on whether or not temperature (T), oxygen (O), or oxygen and temperature (OT) were characterized as potentially limiting or if there was no limitation (N). Note that this is a representative month (October) of DO and temperature data from WOA.

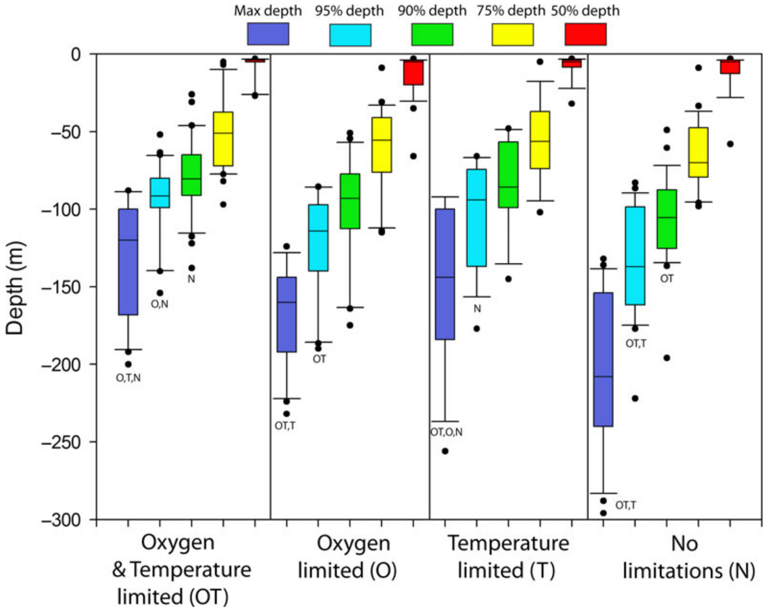


~34% of the data, representing 30 fish, were assigned to the potentially oxygen and temperature limited group (Group OT). The distributions of depths of the 22.8°C isotherm and 3.7 mL L^{-1} DO isopleth in groups with potential environmental limitations were not significantly different, nor were the distributions of these depths in non-limited groups (Kruskal–Wallis, $P > 0.05$, Supporting Information Fig. S2), indicating that the depths of low oxygen and temperature conditions were consistent across the limited groups as well as non-limited groups (i.e., the distribution of oxygen threshold depths was the same in the oxygen & temperature shoaling group and oxygen shoaling group).

The depth distribution of blue marlin was shallowest (Fig. 5) in areas where both temperature and oxygen were potentially limiting (Group OT). Under these conditions, the maximum depth was shallower than all other groups, the 95% depth was shallower than the oxygen limited (Group O) and no limitation (Group N) groups, and the 90% depth was shallower than the no limitations (Group N) group (Kruskal–Wallis, $P < 0.05$). The extent of vertical habitat compression was similar in group O and T, although it was slightly greater in group T as the 95% depth of that group was not significantly different from group OT and the max depth and 95% depths were significantly shallower than group N (Kruskal–Wallis, $P < 0.05$). Vertical habitat compression in Group O was intermediate between T and N, although it was more similar to Group N. It should be noted that the temperature threshold data represents *in situ* conditions as it was based on PAT tag data. The oxygen data will have more uncertainty associated with it as it is based on climatological WOA data, but it can still be used to identify areas where marlin would more likely encounter shoaling of low oxygen waters. Despite this limitation, the fact that vertical habitat compression was greatest in group OT indicates that the vertical distribution of blue marlin was most truncated in areas where both temperature and low oxygen were potentially limiting physiological performance, suggesting that the cumulative impact of low oxygen and temperature was greater than either factor alone.

In addition to vertical habitat compression, we found some evidence of geographical habitat compression driven by the ENSO cycle. Except for 2010, blue marlin moved across the equator during every year of tagging (Figs 1 and 6). In 2009 60% of tagged fish crossed the equator, 2011 33%, 2012 22%, and in 2013 40% of fish tagged in Hawaii, and 29% tagged in Tahiti crossed the equator. The average date of crossing the equator was approximately 19 Oct. (±25 days SD, Sep. 24–Nov. 13), but occurred as early as 12 Sept. and as late as 29 Nov. Strong La Niña conditions existed in 2010, with increased equatorial upwelling, cooler water temperatures and a pronounced cold tongue that extended well into the equatorial Central Pacific. During the 2010 La Niña, blue marlin did migrate south, but upon hitting the cooler waters at the northern edge of the cold tongue their southerly movements ceased and they remained to the north in warmer waters. This suggested that either cold surface

Figure 5. Median maximum, 95%, 90%, 75%, and 50% depths of each tagged marlin in each of the four different habitat groups (n = 30 fish OT, n = 24 fish O, n = 16 fish T, n = 25 fish N). Habitat groups include areas where (i) oxygen and temperature are potentially limiting (OT), (ii) oxygen is limiting (O), (iii) temperature is limiting (T), and (iv) no limitations based on temperature or oxygen (N). Habitats with significant differences ($P < 0.05$) in blue marlin depth are indicated below each boxplot in each habitat. Pairwise comparisons are for each particular depth metric. There were no significant differences in median 75% or 50% depths of marlin in the different habitats. The box denotes median and interquartile range, whiskers show 5th and 95th percentiles, points outliers. Note that temperature data are based on *in situ* temperature data from tags, while oxygen data are the best estimate based on monthly climatological data from WOA.



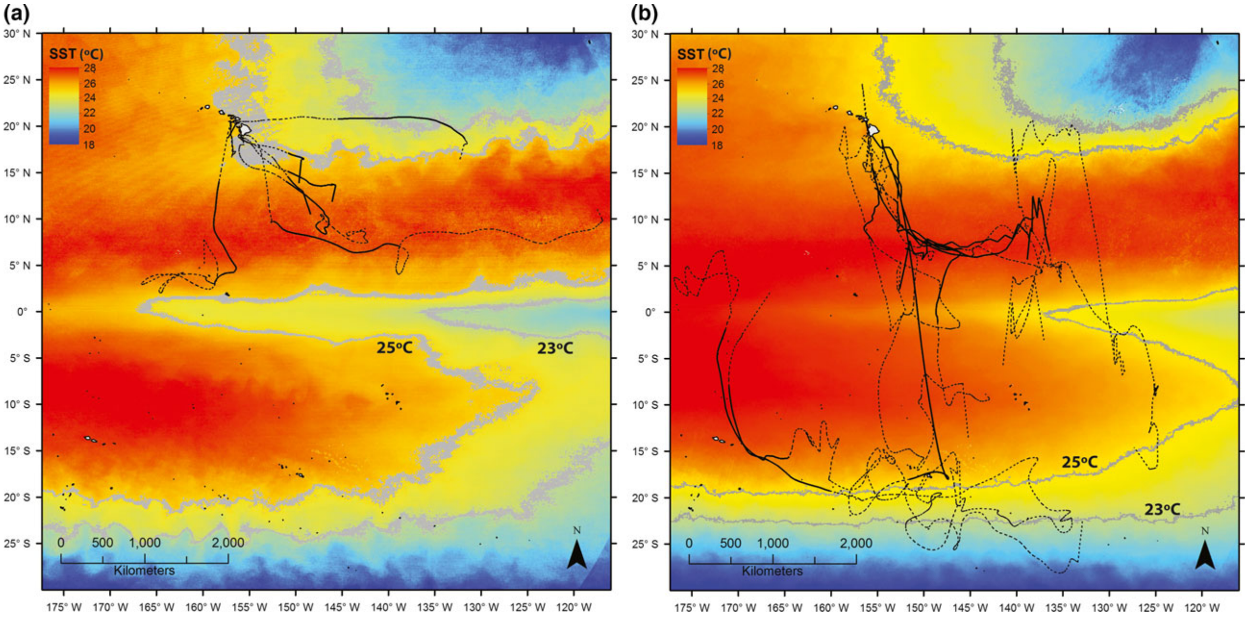
water (e.g., <24°C) creates a thermal barrier to their horizontal migration, that strong upwelling, such as that along the equator during a La Niña, compresses their vertical habitat, or that the two in conjunction restrict their movements at the surface and at depth. Six of the nine fish tracked during 2010 were tracked during the period when marlin typically crossed the equator (24 Sep. to 13 Nov.). In addition, the mean track duration (DAL in Table 1, mean 110, 73, 79 and 68 days for 2009–2012 respectively) was very similar across years (except for 2013 which had longer tracks owing to the use of miniPATs), as was mean pop-up date (11/16, 10/21, 10/23, and 10/24 for 2009–2012, respectively), indicating that differences in the timing and duration of tracks was not influencing our ability to observe movements across the equator.

DISCUSSION

The collection of a unique long-term tagging dataset by the IGMR provided a unique opportunity to study the long-term patterns of movement and habitat use of blue marlin in the Central Pacific and observe the effects of variability in environmental conditions, ranging from smaller-scale seasonal variability to longer-term changes such as those associated with the ENSO cycle, on the horizontal and vertical distribution of this important pelagic predator. In this paper, we demonstrated that both temperature and dissolved oxygen compress vertical habitat, with the extent of compression being greatest when both oxygen and temperature are limiting. We also noted that the horizontal distribution of blue marlin is influenced by SST and that their migratory behavior may be influenced by large-scale fluctuations in SST, in particular, those associated with strong La Niña conditions. This collaboration between Stanford University, the IGFA, and the numerous captains, crews and anglers demonstrates the utility of this type of citizen science-based approach, and it was only through the active engagement and support of the IGFA and captains, crews and anglers of the HIBT that such a large, and long-term electronic tag dataset was able to be collected.

Over the 5 years of tagging, blue marlin exhibited a remarkably consistent overall bimodal pattern of habitat use. Because the tags were programmed to bin data

Figure 6. Trans-equatorial movements of blue marlin during the 2010 La Niña (a) and during the non-La Niña years of the study (2009, 2011, 2012, and 2013, b). Remotely sensed sea surface temperature (GOES Imager, http://oceanwatch.pfeg.noaa.gov) is from September 2010 (a) and is the mean sea surface temperature (SST) for September for 2009, 2011, 2012, and 2013 (b). All tracks are shown for the La Niña year (2010), while only trans-equatorial tracks are shown for the non-La Niña years, with the thick sections showing period of track corresponding to the period of the SST data and dotted lines showing periods of track from before and after September. Note that fish crossed the equator during every year of tagging except for during the 2010 La Niña (see Fig. 1). The 23°C and 25°C isotherms are shown.



into 24-h intervals, we were unable to directly observe diel changes in their depth distribution. However, more recent tag data from this study location (A.B. Carlisle, unpublished data) show that the pattern is a diel one, where blue marlin remain in shallow, warm waters during the night and spent more time at deeper, colder depths and moved throughout the water column during the day. This diel bimodal depth distribution is consistent with findings from earlier studies from Hawaii (Holland *et al.*, 1990; Block *et al.*, 1992a) as well as the Atlantic and Gulf of Mexico (Kerstetter *et al.*, 2003; Kraus and Rooker, 2007; Goodyear *et al.*, 2008), where the nocturnal surface-oriented behavior has been associated with a quiescent state, and the increased depth and diving behavior during the day has been associated with foraging. Block *et al.* (1992b) noted that the blue marlin in Hawaii swam slowly when near the surface but that their speed increased when diving, reaching speeds as high as 225 cm s^{-1} during rapid vertical excursions, which is also consistent with deep dives and deeper daytime depths potentially being associated with foraging (Goodyear *et al.*, 2008). Blue marlin have cranial endothermy, where counter-current heat exchangers and thermogenic tissue that has evolved from extraocular muscle fibers allow for heat to be generated and retained in the brain and eye regions (Block, 1986, 1994; Fritsches *et al.*, 2003). This allows them to be effective visual predators in the deeper, colder waters they might encounter when diving.

Temperature has long been recognized to limit the vertical distribution of pelagic fishes, including tunas and marlin (Green, 1967; Brill *et al.*, 1993; Hinton and Nakano, 1996). Previous studies have documented hypoxia-based vertical habitat compression in billfish (Prince and Goodyear, 2006; Stramma *et al.*, 2012), although these studies focused on eastern boundary currents of the tropical Pacific and tropical Atlantic where persistent and intense upwelling creates large areas where low oxygen and low temperature waters commonly shoal (Helly and Levin, 2004). The relative impact of temperature and oxygen on habitat use will depend on species-specific physiological characteristics (Brill, 1994; Ekau *et al.*, 2010; Seibel, 2011). What has been lacking to date in prior analyses is empirical data documenting the relative importance of temperature and oxygen in influencing the vertical distribution of blue marlin and other pelagic fishes (Brill, 1994).

Our results indicate that the extent of vertical habitat compression is greatest when both oxygen and temperature limitations co-occur, although there was significant compression when just temperature was limiting as well. The maximum depth of blue marlin in areas where the temperature was limiting (group T) was shallower than in areas where oxygen was limiting (group O) or neither oxygen or temperature was limiting (group N), but deeper than blue marlin in areas where both oxygen and temperature were limiting (group OT). This indicates that although low temperature does truncate the vertical distribution of blue marlin, the impact on blue marlin habitat use appears to be greatest when low oxygen and temperature conditions occur together. The lack of significant differences in the depth distribution of blue marlin in group N and the group O is likely a reflection of the lack of *in situ* dissolved oxygen data. Indeed, there was a clear trend in the maximum depth being shallower in group O relative to group N (Fig. 6). It is very likely that with *in situ* dissolved oxygen data the relative importance of dissolved oxygen will be as great if not greater than that of temperature. *In situ* dissolved oxygen and temperature data from tagged fish are required to fully evaluate the relative importance of temperature and oxygen in limiting the vertical distribution of pelagic fishes. Although we are currently limited to estimating the dissolved oxygen levels that the blue marlin experienced from climatological data, with the recent development and continued improvement of dissolved oxygen PAT tags (Coffey and Holland, 2015), this hypothesis may soon be able to be more directly addressed.

Although there was evidence of vertical habitat compression, its effects were relatively subtle as it primarily truncated the deepest parts of the blue marlins' depth distribution (max depth, 95% depth) and did not influence the overall vertical distribution of blue marlin within the mixed layer where they spent the large majority of their time. Even in areas where habitat compression was most extensive, there was no significant difference in the distribution of blue marlin within the depths at which they primarily resided (<100 m, Table 2). Given that blue marlin may be foraging at deeper depths during the day and resting in warmer waters at the surface at night (Goodyear *et al.*, 2008), this reduction in depth distribution would primarily impact them during the daytime hours when they are diving to deeper depths. This limitation may reflect physiological limitations of blue marlin and/or their prey.

It is likely that even in this remote oceanic region of the central Pacific, which is far from the Eastern tropical Pacific where a shallow OMZ is a consistent and dominant oceanographic feature (Helly and Levin, 2004; Gilly *et al.*, 2013), that blue marlin encounter physiological barriers to their vertical and horizontal movements. The minimum average level of dissolved oxygen encountered by tagged blue marlin based on WOA climatological data, which we used as the threshold value to identify potential oxygen limitation, was 3.7 mL L^{-1}. This level is very similar to the 3.5 mL L^{-1} threshold that has been reported to induce stress in tropical pelagic fish (Ingham *et al.*, 1977; Bushnell and Brill, 1991; Prince and Goodyear, 2006) but still above levels reported to be lethal for tunas (0.4–2.16 mL L^{-1}) (Brill, 1994). Although there are no data on the metabolic rate of blue marlin, the metabolic rates of other high-performance pelagic fishes such as tunas and sailfish are high (Dewar and Graham, 1994; Brill, 1996; Idrisi *et al.*, 2002) and blue marlin metabolic rates and oxygen requirements are assumed to be similarly high (Prince and Goodyear, 2006). Hence, it is plausible that dissolved oxygen levels around or below the threshold value used in this study may indeed represent a barrier to blue marlin, but more research is required on metabolic requirements and physiological capabilities of billfishes.

Oceanographic conditions in the central Pacific may present physiological impediments to blue marlin movements in areas not only containing minimal dissolved oxygen, but also cool water. At low temperatures oxygen binds more favorably to hemoglobin, limiting that available for offloading (Weber *et al.*, 2010), the effects of which may be exacerbated in hypoxic waters where there is less oxygen to be diffused across the gill surface into the blood. Additionally, low temperatures have been shown to clearly inhibit cardiac function (Blank *et al.*, 2002, 2004) in pelagic fish by reducing cardiac output. While blue marlin cardiac tissue remains unstudied, the cardiac muscle most likely functions similarly to other pelagic species that exhibit reduced contractility in the cold (Blank *et al.*, 2002). Thus diving into cooler waters may, as in other pelagic fish, induce bradycardia and decrease available oxygen flowing to essential tissues (Blank *et al.*, 2004).

Much like how the vertical distribution of blue marlin is influenced by environmental conditions, their broad migratory patterns also appear to be influenced by oceanographic conditions, in particular, SST (Anraku and Yabuta, 1959; Howard and Ueyangi, 1965; Hinton and Nakano, 1996). Over the course of the 5 years of tagging in Hawaii, tagged blue marlin consistently migrated in a south/southeasterly direction, often moving to the vicinity of French Polynesia. Why blue marlin were not observed to move to the north of the Hawaiian Islands is unclear. The Hawaiian Islands are approaching the northern extent of blue marlin distribution (Nakamura, 1985; Collette *et al.*, 2011), and it may be they did not move to the north because of the overall cooler SSTs that occur to the northeast of the island chain during the autumn and winter (Figs 4 and 6). Of the fish tagged in French Polynesia, two made trans-equatorial movements in a northwesterly direction. Interestingly, the directionality of these trans-equatorial movements is consistent with previous observations. Anraku and Yabuta (1959) noted that blue marlin moving north across the equator moved in a north-westerly direction, while fish crossing the equator in a southerly direction moved in a south-easterly direction, suggesting these movements of tagged fish may reflect a broader migratory pattern.

The only tournament event in the 5 years of tagging in Hawaii that resulted in no blue marlin crossing the equator was the 2010 event, which occurred during a La Niña year. The cold phase of the ENSO cycle (La Niña) is associated with a strengthened westward flow of the South Equatorial Current, which leads to increased equatorial upwelling, shoaling of the thermocline and oxycline, cooler SSTs, and an overall extension of the cool SST water mass from the eastern Pacific (cool tongue) into the Central Pacific (Wyrtki, 1975; Philander, 1989). During this La Niña year, blue marlin moved south and encountered the western extension of the cool tongue, with SSTs ranging from 21 to 24°C from east to west in this region (Fig. 6b). This appeared to present a barrier that they were not willing or able to cross, which is consistent with previous studies showing their preference for warmer temperatures (Holland *et al.*, 1990; Graves *et al.*, 2001; Su *et al.*, 2011a). Upon encountering the cool SSTs, the blue marlin ceased their southern migratory movements and remained in the warm waters to the north of this cold oceanographic feature with fish moving along the northern boundary of this feature.

The cold SSTs prevalent in the equatorial waters during La Niña and the shoaling of the thermocline and oxycline resulting from enhanced upwelling may create a physiological barrier between Hawaii and French Polynesia that blue marlin cannot cross during these conditions. In contrast, El Niño causes elevated SST and decreased upwelling, resulting in an increased mixed layer depth, which reduces physiological stresses at the surface and depth, thereby enabling trans-equatorial blue marlin migrations both directly south and well to the southeast of Hawaii. Also, during neutral years (non El Niño and non La Niña years) blue marlin are not precluded from traversing the equator as in La Niña. The large shifts in SST between the ENSO phases are exemplified by the longitudinal differences in isotherm location. For example, in September of the moderate 2009 El Niño the 25°C isotherm extended only to ~127°W along the equator, while during the strong 2010 La Niña it extended to ~167°W, which represents a nearly 4500 km difference. By dramatically altering the SST and thermo- and oxycline depth, the prevailing ENSO phase likely influences not only the likelihood of trans-equatorial migrations during a given year but also the extent of vertical habitat compression. We hypothesize that this shoaling of low temperature and oxygen conditions and cool SSTs that occur in equatorial waters during La Niña events may present both a vertical and horizontal barrier to blue marlin trans-equatorial movements in the Central Pacific.

The presence of an oceanographic barrier to the movement of blue marlin may have important implications for the population dynamics and migratory behavior of this species, particularly if it hinders important feeding or reproductive migrations. Lee *et al.* (2014) reported that blue marlin are susceptible to localized depletion because of overfishing when mixing rates are not adequate to maintain a constant population density. This issue may be exacerbated when oceanographic barriers reduce connectivity between regions and interrupt potential spawning/foraging migrations. While there remains much uncertainty about the impacts of climate change on future ocean conditions, recent research has suggested that there will be an increase in the frequency of extreme El Niño and La Niña events (Power *et al.*, 2013; Cai *et al.*, 2014, 2015). Any increase in the intensity or frequency of La Niña events will likely create more years with barriers to the movement of blue marlin and decreases in available habitat. This potential reduction in habitat would not only restrict their geographic distribution, but also their vertical distribution because of increased upwelling and shoaling of the oxycline and thermocline associated with La Niña conditions.

The relative impact that such a vertical and horizontal barrier would have on the population dynamics of blue marlin would depend on the persistence of such a barrier, the longitudinal extent of the barrier, as well as the nature of the latitudinal migrations exhibited by blue marlin. Blue marlin are believed to move to Hawaiian waters during the summer to spawn, drawn by the unique oceanographic conditions associated with the island chain (Hopper, 1990; Seki *et al.*, 2002), but why they generally move south/southeast following this spawning period, often moving across the equator towards French Polynesia, remains unclear. These southern migrations after the summer spawning period around Hawaii are consistent with previous research that has shown that blue marlin exhibit a latitudinal shift in their distribution, moving towards higher latitudes during the summer and lower latitudes during the winter (Nakagome, 1958; Anraku and Yabuta, 1959; Su *et al.*, 2008). These broad-scale migratory patterns likely reflect foraging and reproductive migrations (Shimose *et al.*, 2009, 2012). Spawning is believed to occur year-round in equatorial waters, and one hypothesis of why blue marlin make these trans-equatorial migrations is that blue marlin may move to the waters around French Polynesia for reproductive purposes, as this region has been reported to be another spawning location (Howard and Ueyangi, 1965). However, these southern migrations may be related to foraging as well and until more information is obtained the purpose of these trans-equatorial migrations may remain unresolved.

In the western Pacific, blue marlin undertake large foraging migrations after spawning, moving to more productive areas to feed and increase their body condition following the energetically expensive spawning season (Shimose *et al.*, 2009). Although we have demonstrated connectivity between the Hawaiian Islands the French Polynesia, more research is needed to elucidate the function of these migrations. Additionally, further work should be done to determine the pattern and degree of connectivity between the blue marlin of the western, central, and eastern Pacific. Such research would inform a more comprehensive understanding of the entire Pacific Ocean's blue marlin population structure, reproductive ecology, and conservation status.

In addition to providing insight into the biology and ecology of a species, information on the patterns of movement, habitat use and environmental preferences of marine species is needed to generate effective management strategies and understand vulnerability to fishing pressure, especially in wide-ranging pelagic species such as the blue marlin which can move across vast regions of the ocean. Information on distribution, habitat use and environmental preferences of a species can be incorporated into stock assessments (Hinton and Nakano, 1996; Cope and Punt, 2011; Su *et al.*, 2011b) as well as habitat models, which can be used to understand and predict how a species might react in response to a changing climate (Hazen *et al.*, 2013). In this study, we provided information on long-term patterns of habitat use, as well as the variable effects of the different ENSO phases on migratory behavior, of blue marlin in the Central Pacific as well as the influence that oxygen and temperature play in determining the vertical and horizontal distribution of blue marlin. This is the first time that vertical habitat compression has been documented in a billfish outside of the relatively persistent hypoxic zones of the eastern tropical Pacific and Atlantic, extending our understanding of vertical habitat compression to areas outside of these extreme habitats, as well as providing evidence of the relative importance of temperature and oxygen in determining the extent of vertical habitat compression. This is important if we are to understand the ecology of these species, predict how they may respond to the expansion of the OMZs and other effects of climate change, as well as better understand their population dynamics and susceptibility to fisheries.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1. An example of how different depth metrics were calculated from binned time at depth data.

Figure S2. Distribution of depths of the temperature (22.8°C) and oxygen (3.7 mg L^{-1}) threshold depths in different habitat groups.

Figure S3. Depths of 22.8°C isotherm and 3.7 mL L^{-1} DO isopleth for each day of the entire dataset, showing how habitat categories were defined.