Expansion of oxygen minimum zones may reduce available habitat for tropical pelagic fishes

Lothar Stramma[1]*, Eric D. Prince[2] *[+], Sunke Schmidtko[3]*, Jiangang Luo[4], John P. Hoolihan[5], Martin Visbeck[1], Douglas W.R. Wallace[1,6], Peter Brandt[1], & Arne Körtzinger[1]

[1]Leibniz Institute of Marine Sciences IFM-GEOMAR, Düsternbrooker Weg 20, 24105 Kiel, Germany

[2]National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Fl 33149, USA

[3]National Oceanic and Atmospheric Administration, Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE, Seattle, Washington 98115, USA: now at: School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, United Kingdom.

[4]Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

[5]Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School for Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149, USA

[6]Canada Excellence Research Chair, Oceanography Department, Dalhousie University, Halifax, Nova Scotia, B3H 4R2, Canada

*These authors contributed equally to this work.

[+]Corresponding author: eric.prince@noaa.gov

Climate model predictions[1,2] and observations reveal[3,4] regional declines in oceanic dissolved oxygen (DO), which are likely influenced by global warming[5]. Studies indicate on-going DO depletion and vertical expansion of the oxygen minimum zone (OMZ) in the tropical northeast Atlantic Ocean[6,7]. OMZ shoaling may restrict the useable habitat of billfishes and tunas to a narrow surface layer[8,9]. We report a decrease in the upper ocean layer exceeding 3.5 mL L^{-1} DO at a rate of ≤ 1 m yr^{-1} in the tropical northeast Atlantic (0-25°N, 12-30°W), amounting to an annual habitat loss of ~$5.95 \times 10^{13} m^3$, or 15% for the period 1960-2010. Habitat compression was validated using electronic data from 47 blue marlin. This phenomenon increases vulnerability to surface fishing gear for billfishes and tunas[8,9], and may be associated with a 10-50% worldwide decline of pelagic predator diversity[10]. Further expansion of the Atlantic OMZ along with overfishing may threaten the sustainability of these valuable pelagic fisheries and marine ecosystems.

Dissolved oxygen (DO) is critical for sustaining most marine animal life. When DO is minimized, widespread mortality[11,12] or avoidance[13] of affected areas can result. Oxygen Minimum Zones (OMZs) in the eastern tropical seas represent the largest contiguous areas of naturally occurring hypoxia[9] in the world's oceans. In the current climate change cycle, characterized by anthropogenic CO_2 emissions[2] and global warming, these areas are expanding and shoaling[3,12,14]. Possible consequences of OMZ expansion to the marine ecosystem[14] include loss of vertical habitat for high oxygen demand tropical pelagic billfishes and tunas and the associated increased risk of overfishing of these species by surface fishing gear[8,9].

Large scale expansion of OMZs over the previous 50 years[3] poses a challenge for predicting impacts to pelagic fish stocks and their ecosystem. Although oceanographic modelling and ocean observations for retrospective analyses are useful for examining past trends, understanding future OMZ expansions and the concurrent impacts on billfish and tuna populations are essential for preventing overfishing. We analyzed recent hypoxia data associated with OMZ expansion in the eastern tropical Atlantic (ETA) to examine possible habitat loss of the near surface layer. Additionally, we present vertical habitat use data of Atlantic blue marlin (*Makaira nigricans*) monitored with electronic tags (Fig. 1). Changes in utilized habitat were validated by maximum daily depths (MDDs), whereby increasingly deeper exploration was evident outside the OMZ (where DO remains elevated), compared to inside the OMZ (where DO decreases with depth).

Here, habitat loss associated with OMZs (termed hypoxia-based habitat compression) is characterised as the diminishing of the oxygenated shallow surface mixed layer above a threshold of cold hypoxic water. As a reference benchmark, we defined the OMZ as the areas where sub-thermocline DO levels are $\leq$ 3.5 mL L^{-1} (~150 µmoL kg^{-1})[8] with regard to this species grouping[15,16,17]. This threshold has been reported[8,9,16,17] as a plausible lower habitat boundary for billfishes, tropical tunas, and other tropical pelagic fishes, although occasional short-duration deeper dives occur[9]. While DO requirements of individual species vary depending on their mode of respiration, metabolic and physiological requirements[18], DO levels $\leq$3.5 mL L^{-1} may induce stress symptoms reaching lethality over prolonged exposure for high oxygen demand billfishes and tunas [15,19], thus potentially restricting their depth distribution to the oxygenated near surface layer[8,9].

Tropical pelagic tunas and billfishes exhibit a high performance physiology[17], including exceptionally high rates of somatic and gonadal growth, digestion, and rapid recovery from exhaustive exercise. These energy consuming expenditures require large amounts of oxygen[15,17]. Direct oxygen tolerance measurements for adult billfishes are not available, though one juvenile sailfish (*Istiophorus platypterus*) study indicated high oxygen consumption and typical metabolic rates associated with tropical tunas [19]. These high oxygen demand species also share obligate ram ventilation respiration, large gill surface, and DO tolerances[15,17,20,21]. Here, we consider the plausible hypothesis that these species have oxygen limitations that impact vertical habitat use.

A major consequence of habitat compression is increased vulnerability to overfishing by surface fishing gear[8,9]. Because most Atlantic billfishes and tunas are at least fully exploited, if not over-fished[8,9,22], any OMZ expansion would potentially exacerbate this situation. Synergism between current climate change, OMZ expansion, and ocean acidification may contribute further to reducing useable habitat for these species[9].

We constructed maps from DO data sampled since 2005, and historical data from HydroBase-2 (See Supplementary Information). We also constructed isobaric maps of a northern subarea of the ETA (0°N to 25°N, 12°W to 30°W), from data collected through December 2009. The thermocline depth ranged from 25-50 m near the African shelf to 100 m in the western ETA, deepening rapidly at its boundary transition point (Fig. 2a) between the tropical Atlantic and subtropical gyre. High variability of thermocline depth due to seasonal and inter-annual upwelling renders any trend analysis in the areas close to the shelf and coastline uncertain. The thermocline depth is most pronounced around 10-15°N off West Africa, weakening as it extends offshore[6]. A notable western expansion of the

ETA OMZ (at 125 m) extends nearly to the coast of Guyana (10°N, 60°W, Fig. 2a), while vertical expansion has resulted in habitat loss estimated at ≤1 m yr^{-1} since 1960 (Fig. 2b). The most noticeable growth of the OMZ is the horizontal expansion along the northern and southern boundaries. The rate of DO change at the depth of the 3.5 mL L^{-1}, as derived for 2010, indicates a decrease of as much as 0.022 mL L^{-1} yr^{-1} (Fig. 2c).

Upper limits of the OMZ (1960-2010) were sorted and evaluated by each grid point. The summed area indicated threshold shoaling over the fifty year interval for the area of recent data collection, in addition to revealing the corresponding habitat loss (Fig. 2d) and its average percentage over the cumulative area (Fig. 2e). Habitat compression is more prominent at the northern and southern side of the ETA OMZ, the same areas exhibiting recent expansion. The estimated annual habitat loss for area 0-25°N, 12-30°W, assuming a maximum habitat depth of 500 m, is 5.95×10^{13} m^3. Given the ETA OMZ expansion (Fig. 2a), along with expected similar DO trends[3], the resultant habitat loss is assumed to be much larger than the estimates presented for the selected subarea. Oxygen depletion over the last 50 years is congruent with upper ocean warming since 1950[23] and fluctuating DO levels caused by changes in zonal jet strength within the ETA[24].

Horizontal and vertical movements of 47 blue marlin[9] (Fig. 1, and Supplementary Table 2) were monitored with pop-up satellite archival tags (PSATs); 10 deployed in the ETA and 37 in the western North Atlantic (WNA). A plot of MDDs encountered, versus DO levels at 100 m, clearly showed that blue marlin ventured deeper when DO levels >3.5 mL L^{-1} were available (Fig. 3a). In addition, we illustrate a transition of vertical habitat use by comparing MDDs in the WNA, where ample DO does not limit diving depth, to the ETA, where DO is progressively more limited with depth moving eastward (Fig. 3b-f). Oxygen data displayed in Figure 3b-f are the local weighted mean, tri-cubed weights applied to match the season (120 days maximum radius), location (4° maximum latitudinal radius), and decade (20 yr maximum radius). A clear link between the oxygen distribution and the MDDs encountered was evident for all blue marlin. In the OMZ-free WNA, blue marlin often descended to depths >200 m (Fig. 3b, 3d). In contrast, one blue marlin in the ETA moved northwest, remaining in the upper 100m while inside the OMZ (Fig. 3c, 3e), then explored depths >200 m after exiting the OMZ. The second blue marlin monitored in the ETA remained in the coastal region of the OMZ where hypoxia was more severe (Fig. 3c 3f), spending most of its time at depths $\leq$100 m.

Our results revealed that DO levels have decreased across large areas of the subsurface ETA, and that recent shoaling of these layers is evident along the northern, southern and western boundaries of the OMZ. The DO decrease in the ETA is an on-going process with local trends on the order of -0.01 mL L^{-1} yr^{-1} (Supplementary Information). The low DO levels appear to restrict the vertical movement of blue marlin in the habitat compressed areas, as depicted by the maximum daily depths encountered before and after transiting the OMZ boundary (Figure 3e). In the WNA, no DO $\leq$3.5 mL L^{-1} exists in the upper 800 m, allowing greater vertical habitat use (Fig. 3d). In the ETA, where DO levels decrease moving eastward, the maximum depths encountered by blue marlin also decreased, as the fish appear to be restricted to the more oxygenated water near the surface (Fig. 3e-f). Habitat compression also impacts the preferred prey of billfishes and tunas (primarily small scombrids, cluepids, and carangids), which share similar high oxygen demand physiology[20,25,26]. Hence, these pelagic predators and their preferred prey tend to be compressed together in the oxygenated narrow surface mixed layer habitat above the thermocline[8,9]. Oceanic hypoxia can impact food pathways within the pelagic ecosystem[18] by decoupling predators from their prey, or putting them in closer proximity to each other as reported in the ETA and eastern tropical Pacific (ETP) OMZs[8,26]. For example, average size of sailfish landed in the ETA and ETP have been consistently larger compared to those caught in non-compression areas, a result attributed to increased proximity to prey[8,9]. Intense coastal upwelling occurring in the ETA and ETP contributes to increased primary and secondary productivity[27], which ultimately may influence the carrying capacities for billfishes and tunas residing above the OMZs. Information regarding trophic impacts on epipelagic communities resulting from OMZ expansion, particularly those pertaining to carrying capacity, will assist assessment scientists toward more effective management of fish stocks.

Pelagic fishes generally avoid hypoxic conditions[13], although at least one exception is the bigeye tuna (*Thunnus obesus*) that has unique blood oxygen-binding characteristics allowing lower DO tolerances than other tropical tunas[28]. Bigeye tuna often occupy areas below the thermocline in the ETA OMZ during diurnal periods where DO levels are consistently $\leq$3.5 mL L^{-1}, while foraging in the prey abundant surface mixed layer at night. Other predatory species, such as the jumbo squid (*Dosidicus gigas*)[29], reside in the most hypoxic areas of the OMZ, but also migrate to the surface mixed layer to feed. Thus, hypoxia tolerant predators are also impacted by the OMZs due to the increased availability of prey species in the surface mixed layer. Importantly, this increased availability of prey most likely contributes to the restricted vertical habitat use of blue marlin[26].

OMZ expansion is evident in all tropical ocean basins and throughout the subarctic Pacific[14], making habitat compression an increasingly global issue. The prevalence and continued expansion of the OMZ across the tropical Atlantic presents a critical issue regarding the compression phenomenon and management of tropical pelagic fishes[9]. Because many of the targeted and bycatch pelagic species harvested in the OMZ are either fully exploited or overfished[22], any potential fishery impacts related to habitat compression warrant particular attention. Because the ETA OMZ encompasses nearly all Atlantic equatorial waters, the estimated annual loss of vertical habitat (up to 1 m) resulting from continual OMZ expansion represents about $5.95x10^{13}m^3$, equivalent to 15% habitat loss in the upper 200 m between 1960 and 2010 (Fig. 2d). This magnitude of habitat loss could profoundly impact pelagic ecosystems and associated fisheries, particularly for the billfishes and tunas representing some of our most valuable economic resources. High catch rates in habitat compressed areas can falsely signal an overly optimistic population condition for both target species (e.g. tuna) and bycatch species (e.g. blue marlin). Thus, the phenomenon of habitat compression should be taken into account for management decisions pertaining to harvest rates and fishing pressure. Vigilant monitoring of tropical pelagic fish populations in OMZ areas is recommended to insure these stocks are not diminished further. The increased vulnerability and overexploitation of tropical pelagic fishes[9] caught in OMZs raises a particular challenge with regard to the high harvest rates presently taking place in global fisheries[30]. Considering that fishing pressure is likely to continue at a high rate into the foreseeable future, and OMZ expansion is expected to worsen with the current cycle of climate change, associated global warming, and increasing atmospheric CO_2 levels[2,31], any further loss of habitat might be expected to adversely impact the sustainability of these fish stocks.

METHODS SUMMARY

As most of the biological literature presents DO in mL L^{-1}, instead of μmol kg^{-1}, we use the mL L^{-1} unit of measure to illustrate DO levels in this study. HydroBase-2 (See Supplementary Information) quality controlled data as of 10 October 2008 were augmented with additional data sets from recent years (Supplementary Table S1 and Figure S1). To construct the mean 2010 state and trend of DO, vertical high resolution CTD profiles since 1960 are sub-sampled to 8 dbar intervals, then all oxygen data is binned in 0.5° x 0.5° x 10 dbar annual bins to reduce bias due to spatial difference in sampling density. The mean state and trend were mapped on the same grid by applying a least squares linear model (LOESS) at each grid-point to all binned data points with positive weights. Data are weighted by multiplication of two standard tri-cube filters, a horizontal with 440 km radius and vertical with 30 dbar radius. As last step prior mapping an inter quartile range (IQR) filter is applied to the DO data, rejecting values three times the IQR below the lower quartile or three times the IQR above the upper quartile. The radii are increased by 50% for Figure 2a, and trends due to sparse sampling were not computed. The model uses linear and quadratic fits in longitude, latitude, pressure and temperature to determine trend and mean state of DO.

Pop-up satellite archival tags (PSATs) were used to provide a fishery independent means of monitoring horizontal and vertical habitat use of blue marlin[8,9]. In-water tagging techniques, associated equipment, and methods for Kalman filter tracks described in our previous work[8,9] and computations of maximum daily depth presented here are described in more detail in the supplementary information.

1. Bopp, L., Le Quere, C., Heimann, M., Manning, A.C. & Monfray, P. Climate induced oceanic oxygen fluxes: Implications for the contemporary carbon budget. *Global Biogeochem. Cycles* **16**, doi:10.1029/2001GB001445 (2002).
2. Oschlies, A., Schultz, K.G., Riebesell, U. & Schmittner, A. Simulated 21 century's increase in oceanic suboxia in CO_2-enhanced biotic carbon export. *Global Biogeochem. Cycles* **22**, GB4008 doi:10.1029/2007GB003147 (2008).
3. Stramma, L., Johnson, G.C., Sprintall, J. & Mohrholz, V. Expanding oxygen-minimum zones in the tropical oceans. *Science* **320**, 655-658 (2008).
4. Bograd, S.J. *et al*. Oxygen declines and the shoaling of the hypoxic boundary in the California Current. *Geophys. Res. Lett*. **35**, L12607, doi:10.1029/2008GL034185 (2008).
5. Keeling, R.F., Körtzinger, A. & Gruber, N. Ocean deoxygenation in a warming world. *Annu. Rev. Mar. Sci.* **2**, 199-229 (2010).
6. Stramma, L., *et al.* Oxygen minimum zone in the North Atlantic south and east of the Cape Verde Islands, *J. Geophys. Res*., **113**, C04014, doi:10.1029/2007JC004369, (2008).
7. Stramma, L., Visbeck, M., Brandt, P., Tanhua, T. & Wallace, D. Deoxygenation in the oxygen minimum zone of the eastern tropical North Atlantic. *Geophys. Res. Lett*., **36**, L20607, doi:10,1029/2009GL039593, (2009).
8. Prince, E.D. & Goodyear, C.P. Hypoxia-based habitat compression of tropical pelagic fishes. *Fish. Oceanogr.* **15**, 451-464 (2006).
9. Prince, E.D. *et al*. Ocean scale hypoxia-based habitat compression of Atlantic Istiophorid billfishes. *Fish. Oceangr.* **19**(6), 448-462, (2010).

10. Worm, B., Sandow, M., Oschlies, A., Lotze, H.K. & Myers, R.A. Global patterns of predator diversity in the open oceans. *Science* **308**, 1365-1369 (2005).

11. Chan, F. *et al*. Emergence of anoxia in the California Current large marine ecosystem. *Science* **319**, 920 (2008).

12. Diaz, R.J. & Rosenberg, R. Spreading dead zones and consequences for marine ecosystems. *Science* **321**, 926-929 (2008).

13. Randell, D.J. *Fish Physiology. The Nervous System. Circulation, and Respiration* 253-292 (Academic Press, 1970).

14. Whitney, F.A., Freeland, H.J. & Robert, M. Persistently declining oxygen levels in the interior waters of the eastern subarctic Pacific. *Prog. Oceanogr.* **75**, 179-199 (2007).

15. Brill, R.W. A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. *Fish. Oceanogr.* **3**:204-216 (1994).

16. Roberts, J.L. *The Physiological Ecology of Tunas* 83-88 (Academic Press, 1978).

17. Brill, R.W. Selective advantages conferred by the high performance physiology of tunas, billfish, and dolphin fish. *Comp. Biochem. Physiol.* **113**, 3-15 (1996).

18. Seibel, B.A. Critical oxygen levels and metabolic suppression in oceanic oxygen minimum zones. *J.Exper.Biol*., **214**, 326-336. (2011).

19. Idrisi, N., *et al.* Behavior, oxygen consumption and survival of stressed sailfish (*Istiophorus platypterus*) in captivity. *Mar. Fresh. Behav. Physical*. 36:51-57 (2002).

20. Ekau, W., Auel, H., Portner, H.-O., and Gilbert, D. Impacts of hypoxia on the structure and processes in pelagic communities (zooplankton, macro-invertebrates and fish). *Biogeosci.* **7**, 1669-1699. (2010).

21. Wegner, N.C., Sepulveda, C.A., Bull, K.B. & Graham J.B. Gill morphometrics in relation to gas transfer and ram ventilation in high-energy demand teleosts: scombrids and billfishes. *J. Morphol.* **271**, 36-49 (2010).

22. ICCAT (International Commission for Conservation of Atlantic Tunas). Executive summary reports for blue marlin, white marlin, sailfish and yellowfin tuna. *Report for biennial period 2010-2011, part I,* **2**, 12-118 (Madrid, Spain 2011).

23. Domingues, C.M., *et al.* Improved estimates of upper-ocean warming and multi-decadal sea-level rise. *Nature* **453**, 1090-1093 (2008).

24. Brandt, P. *et al*. Changes in the ventilation of the oxygen minimum zone of the tropical North Atlantic. *J. Phys. Oceanogr.* **40**, 1784-1801 (2010).

25. Kreiner, A., Stenevik, E.K., & Ekau, W. Sardine *Sardinops sagax* and anchovy *Engraulis encrasicolus* larvae avoid regions with low dissolved oxygen concentrations in the northern Benguela Current system. *J. Fish. Biol.,* **74**, 270-277 (2009).

26. Goodyear, C.P. *et al.* Vertical habitat use of Atlantic blue marlin *Makaira nigricans*: interaction with pelagic longline gear. *Mar. Eco. Prog. Ser*., **365**:233-245 (2008).

27. Cushing, D. Upwelling and fish production. FAO *Fish. Tech. paper*. **84**:40 pp. (1969).

28. Lowe, T., Brill, R., & Cousins, K. Blood oxygen-binding characteristics of bigeye tuna (*Thunnus obesus*), a high-energy-demand teleost that is tolerant of low ambient oxygen. *Mar. Biol.* **136**, 1087-1098 (2000).

29. Gilly, W.F. *et al.* Vertical and horizontal migrations by the jumbo squid *Dosidicus gigas* revealed by electronic tagging. *Mar. Ecol. Prog. Ser*. **324**, 1-17 (2006).

30. Worm, B. *et al.* Rebuilding global fisheries. *Science* **325**,578-585 (2009).

31. Brewer, P. G. & Peltzer, E.T. Limits to marine life. *Science* **324**, 347-348 (2009).

Correspondence and requests for materials should be addressed to Eric D. Prince, eric.prince@noaa.gov.

Acknowledgements The Deutsche Forschungsgemeinschaft (DFG) provided support as part of the Collaborative Research Center SFB-754 (L.S., M.V., D.W., P.B., A.K.). Support for the biological part of the study was provided through the Southeast Fisheries Science Center, The Billfish Foundation, and the Adopt-A-Billfish Program (E.D.P.). Additional support was provided through the NOAA Climate Program Office and the NOAA Office of Oceanic and Atmospheric Research (S.S.). Support for J.L. and J.P.H. provided by the Cooperative Institute for Marine and Atmospheric Studies (CIMAS), a Cooperative Institute of the University of Miami and the National Oceanic and Atmospheric Administration, cooperative agreement NA1RJ1226.

Author Contributions L.S., E.D.P. and S.S. designed the experiment. E.D.P. and J.P.H. contributed biological expertise and biological data sets. S.S. and J.L. performed the oceanographic and biological computations and did the art work. M.V., D.W., P.B., A.K. contributed data and Atlantic Ocean expertise. E.D.P., L.S., J.P.H. and S.S. wrote the paper. All authors discussed the results and commented on the manuscript.

Additional Information

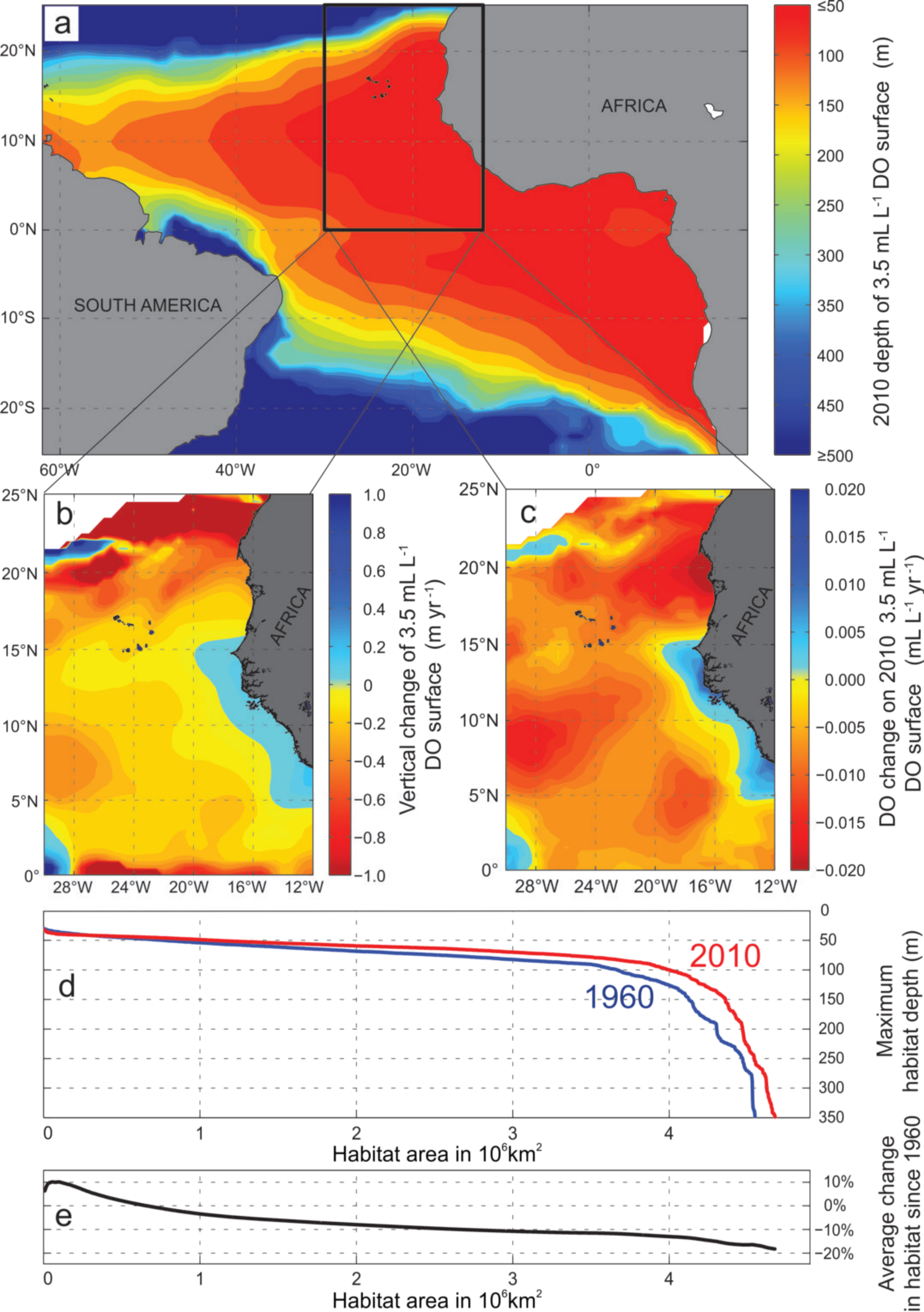
The authors declare no competing financial interests. Supplementary information accompanies this paper on www.nature.com/natureclimatechange. Reprints and permission information is available at http://www.nature.com/reprints. Correspondence and requests for materials should be addressed to Eric D. Prince, eric.prince@noaa.gov.

Figure Legend

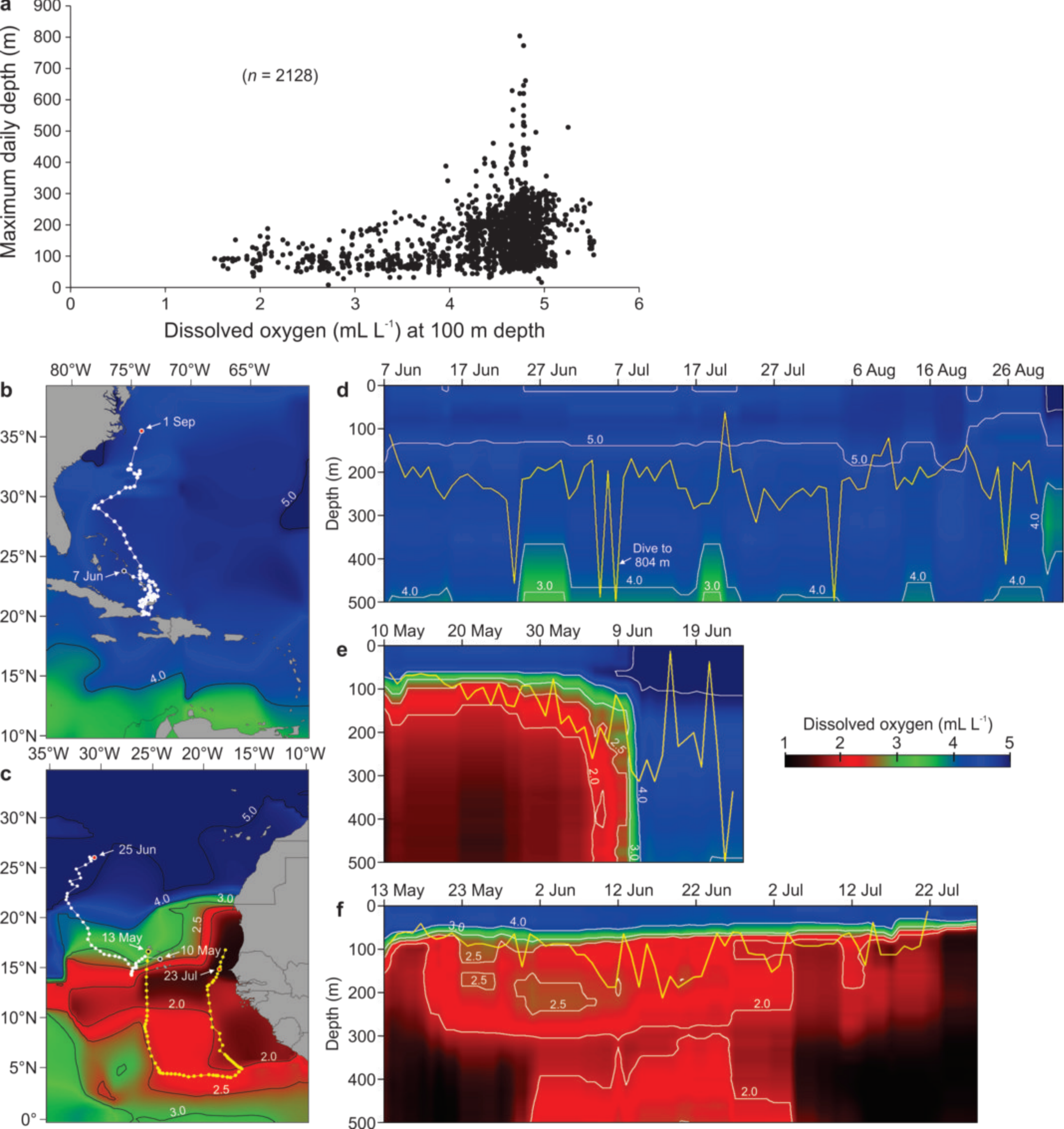
Figure 1| Blue marlin *Makaira nigricans* with a pop-up satellite archival tag used to monitor horizontal and vertical habitat use. As one of the largest teleosts in the Atlantic that grows to nearly 1,000 kg, this high oxygen demand tropical pelagic fish requires dissolved oxygen levels $\geq$3.5 mL L^{-1}. Photo courtesy of Bill Boyce (http://www.savethefish.org/gallery_bill_boyce.htm).

Figure 2 | Eastern Atlantic dissolved oxygen and habitat changes. a, depth of the 3.5 mL L^{-1} DO surface (m) on 1 January, 2010; **b,** average vertical change of the 3.5 mL L^{-1} DO surface 1960 to 2009 (m yr^{-1}: blue deepening); **c,** DO change (mL L^{-1} yr^{-1}) at the depth of the 3.5 mL L^{-1} surface in 2010; **d,** summed area of sorted grid points by depth of 3.5 mL L^{-1} DO level for the region shown in b**; and e,** corresponding average habitat loss relative to the surface over the cumulative area due to the change in d.

Figure 3 | Blue marlin horizontal tracks and maximum daily depths. a, Maximum daily depths (MDD) versus DO at 100 m for 47 blue marlin; **b**, blue marlin track in the western North Atlantic (WNA, 2003); **c,** blue marlin tracks (2) in the eastern tropical Atlantic (ETA, 2004); **d,** MDD versus time in the WNA in 2003 (white track, b); **e,** MDD versus time in the ETA in 2004 (white track, c); and **f,** MDD versus time in the ETA nearest the continental shelf in 2004 (yellow track, c). The mean DO level (mL L^{-1}) at 100 m depth in **b, c,** and **d-f** are from 2004-2005 data.



a
AFRICA
SOUTH AMERICA
2010 depth of 3.5 mL L^{-1} DO surface (m)
≤50
100
150
200
250
300
350
400
450
≥500
b
AFRICA
Vertical change of 3.5 mL L^{-1} DO surface (m yr^{-1})
c
DO change on 2010 3.5 mL L^{-1} DO surface (mL L^{-1} yr^{-1})
d
2010
1960
Maximum habitat depth (m)
Habitat area in 10^{6}km^2
e
Average change in habitat since 1960
Habitat area in 10^{6}km^2


a
Maximum daily depth (m)
(n = 2128)
Dissolved oxygen (mL L-1) at 100 m depth
b
80°W 75°W 70°W 65°W
1 Sep
7 Jun
5.0
4.0
c
35°W 30°W 25°W 20°W 15°W 10°W
25 Jun
13 May
10 May
23 Jul
5.0
4.0
3.0
2.5
2.0
d
7 Jun 17 Jun 27 Jun 7 Jul 17 Jul 27 Jul 6 Aug 16 Aug 26 Aug
Depth (m)
Dive to 804 m
e
10 May 20 May 30 May 9 Jun 19 Jun
f
13 May 23 May 2 Jun 12 Jun 22 Jun 2 Jul 12 Jul 22 Jul
Dissolved oxygen (mL L-1)