

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

Lothar Stramma¹, Eric D. Prince^{2*}, Sunke Schmidt^{3†}, Jiangang Luo⁴, John P. Hoolihan⁵, Martin Visbeck¹, Douglas W. R. Wallace^{1,6}, Peter Brandt¹ and Arne Körtzinger¹

Climate model predictions^{1,2} and observations^{3,4} reveal regional declines in oceanic dissolved oxygen, which are probably influenced by global warming⁵. Studies indicate ongoing dissolved oxygen depletion and vertical expansion of the oxygen minimum zone (OMZ) in the tropical northeast Atlantic Ocean^{6,7}. OMZ shoaling may restrict the usable 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} dissolved oxygen at a rate of $\leq 1 \text{ m yr}^{-1}$ in the tropical northeast Atlantic ($0\text{--}25^\circ \text{ N}$, $12\text{--}30^\circ \text{ W}$), amounting to an annual habitat loss of $\sim 5.95 \times 10^{13} \text{ m}^3$, or 15% for the period 1960–2010. Habitat compression and associated potential habitat loss was validated using electronic tagging 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 diversity¹⁰. Further expansion of the Atlantic OMZ along with overfishing may threaten the sustainability of these valuable pelagic fisheries and marine ecosystems.

Dissolved oxygen is critical for sustaining most marine animal life. When dissolved oxygen is minimized, widespread mortality^{11,12} or avoidance¹³ of affected areas can result. OMZs in the eastern tropical seas represent the largest contiguous areas of naturally occurring hypoxia⁹ in the world's oceans. In the present climate change cycle, characterized by anthropogenic CO_2 emissions² and global warming, these areas are expanding and shoaling^{3,12,14}. Possible consequences of OMZ expansion to the marine ecosystem¹⁴ 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 past 50 years³ 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 is essential for preventing overfishing. We analysed recent hypoxia data associated with OMZ expansion in the eastern tropical Atlantic (ETA) to examine possible habitat loss of the near-surface layer. We also present vertical habitat use data of Atlantic blue marlin (*Makaira nigricans*) monitored with electronic tags (Fig. 1). Changes in habitat use were validated by maximum daily depths



Figure 1 | Blue marlin *M. nigricans* with an electronic 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 $\geq 3.5 \text{ ml l}^{-1}$. Photo courtesy of B. Boyce (http://www.savethefish.org/gallery_bill_boyce.htm).

(MDDs), whereby increasingly deeper exploration was evident outside the OMZ (where dissolved oxygen remains elevated), when compared with inside the OMZ (where dissolved oxygen decreases with depth).

Here, habitat loss associated with OMZs (termed hypoxia-based habitat compression) is characterized 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 subthermocline dissolved oxygen levels are $\leq 3.5 \text{ ml l}^{-1}$ ($\sim 150 \mu\text{mol kg}^{-1}$; ref. 8) with regard to this species grouping^{15–17}. This threshold has been reported^{18,9,16,17} as a plausible lower habitat boundary for billfishes, tropical tunas and other tropical pelagic fishes, but occasional short-duration deeper dives occur⁹. Although dissolved oxygen requirements of individual species vary depending on their mode of respiration, metabolic and physiological requirements¹⁸, dissolved oxygen levels $\leq 3.5 \text{ ml l}^{-1}$ 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}.

¹Leibniz Institute of Marine Sciences IFM-GEOMAR, Düsterbrookweg 20, 24105 Kiel, Germany, ²National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149, USA, ³National Oceanic and Atmospheric Administration, Pacific Marine Environmental Laboratory, 7600 Sand Point Way NE, Seattle, Washington 98115, USA, ⁴Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149, USA, ⁵Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School for Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, Florida 33149, USA, ⁶Canada Excellence Research Chair, Oceanography Department, Dalhousie University, Halifax, Nova Scotia B3H 4R2, Canada. [†]Present address: School of Environmental Sciences, University of East Anglia, Norwich NR4 7TJ, UK. *e-mail: eric.prince@noaa.gov.

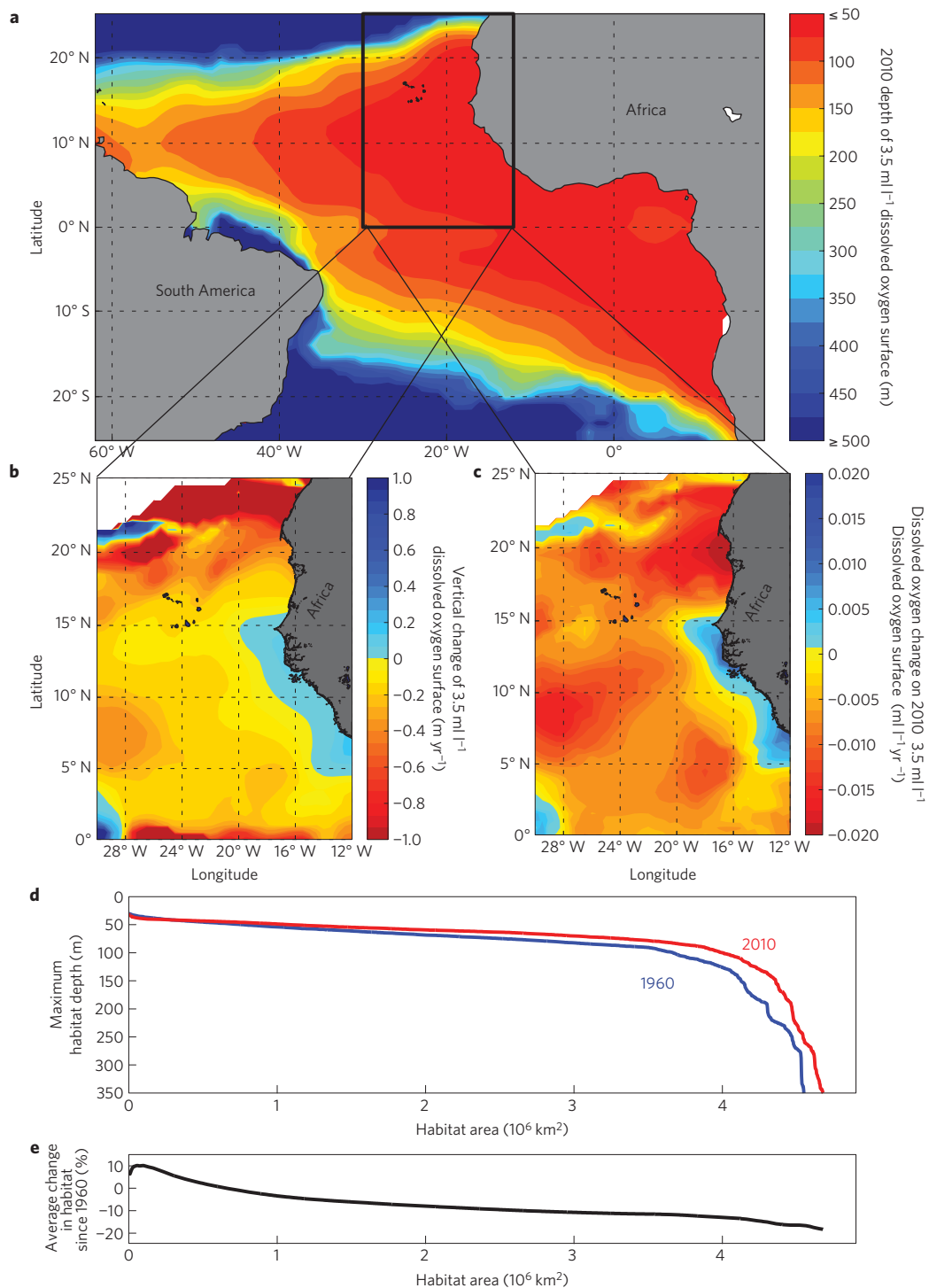


Figure 2 | Eastern Atlantic dissolved oxygen and habitat changes. **a**, Depth of the 3.5 ml l^{-1} dissolved oxygen surface (m) on 1 January 2010. **b**, Average vertical change of the 3.5 ml l^{-1} dissolved oxygen surface 1960–2009 (m yr^{-1} ; blue deepening). **c**, Dissolved oxygen change ($\text{ml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

Tropical pelagic tunas and billfishes exhibit a high-performance physiology¹⁷, 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, although one juvenile sailfish (*Istiophorus platypterus*) study indicated high oxygen consumption and typical metabolic rates associated with tropical

tunas¹⁹. These high-oxygen-demand species also share obligate ram ventilation respiration, large gill surface and intolerance to low ambient dissolved oxygen^{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}. As most Atlantic billfishes and tunas are at least fully exploited, if not

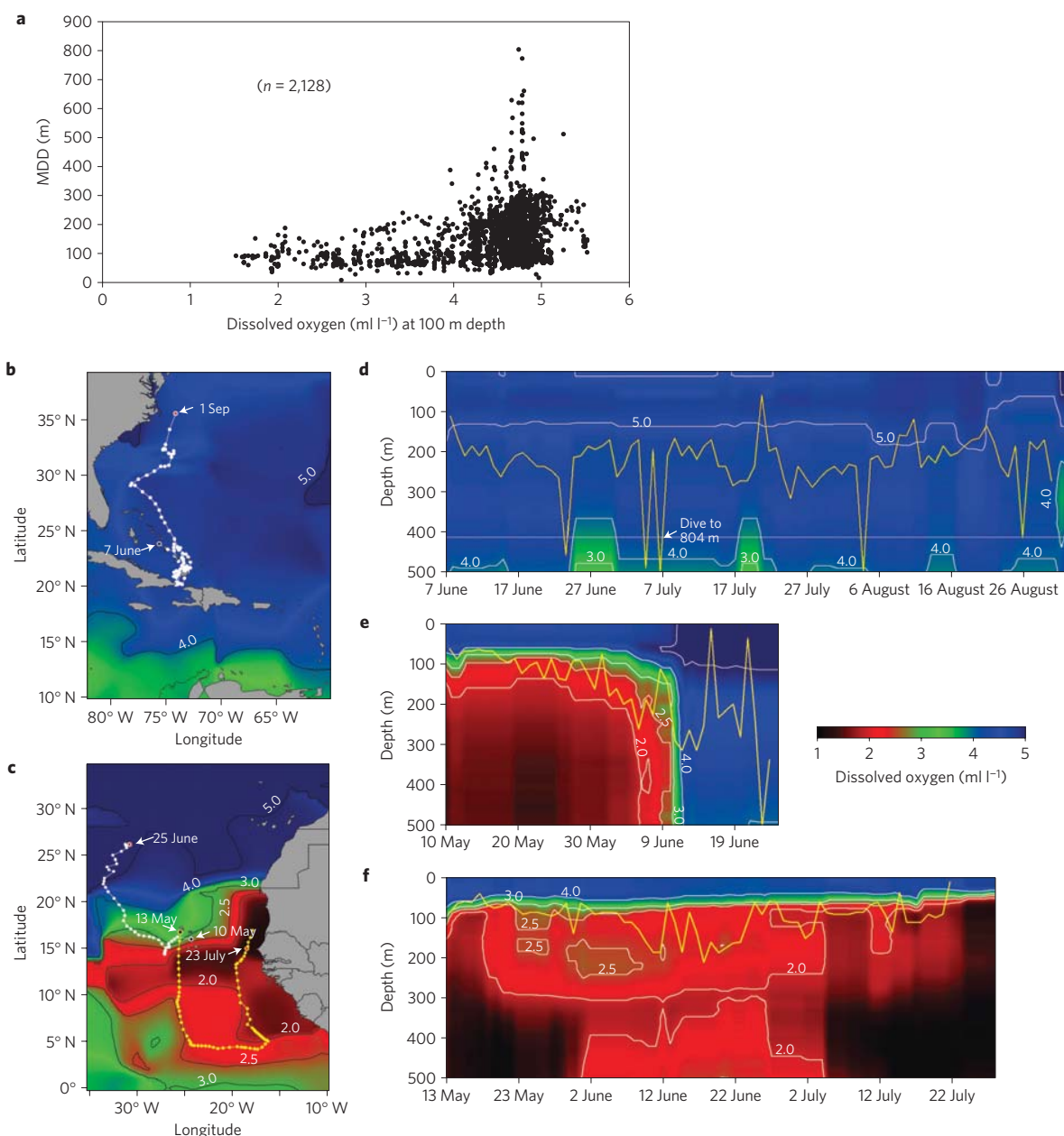


Figure 3 | Blue marlin horizontal tracks and MDDs. a, MDDs versus dissolved oxygen at 100 m for 47 blue marlin. **b**, Blue marlin track in the WNA (2003). **c**, Blue marlin tracks (two) in the ETA (2004). **d**, MDD versus time in the WNA in 2003 (white track, **b**). **e**, MDD versus time in the 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 dissolved oxygen level (ml l^{-1}) at 100 m depth in **b–f** is from 2004–2005 data.

overfished^{8,9,22}, any OMZ expansion would potentially exacerbate this situation. Synergism between present climate change, OMZ expansion and ocean acidification may contribute further to reducing usable habitat for these species⁹.

We constructed maps from dissolved oxygen 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 to 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 interannual upwelling renders any trend analysis in the areas close to the shelf and coastline uncertain. The thermocline depth is most pronounced around

$10\text{--}15^{\circ}\text{N}$ off West Africa, weakening as it extends offshore⁶. A notable western expansion of the ETA OMZ (at 125 m) extends nearly to the coast of Guyana (10°N , 60°W , Fig. 2a), and vertical expansion has resulted in habitat loss estimated at $\leq 1\text{ m yr}^{-1}$ since 1960 (Fig. 2b). The most noticeable growth of the OMZ is the horizontal expansion along the northern and southern boundaries. The rate of dissolved oxygen change at the depth of the 3.5 ml l^{-1} surface, as derived for 2010, indicates a decrease of as much as $0.022\text{ ml l}^{-1}\text{ yr}^{-1}$ (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 50-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 and potential habitat loss 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 the area 0–25° N, 12–30° W, assuming a maximum habitat depth of 500 m, is $5.95 \times 10^{13} \text{ m}^3$. Given the ETA OMZ expansion (Fig. 2a), along with expected similar dissolved oxygen trends³, the resultant plausible habitat loss is assumed to be much larger than the estimates presented for the selected subarea. Oxygen depletion over the past 50 years is congruent with upper ocean warming since 1950 (ref. 23) and fluctuating dissolved oxygen levels caused by changes in zonal jet strength within the ETA (ref. 24).

Horizontal and vertical movements of 47 blue marlin⁹ (Fig. 1 and Supplementary Table S2) were monitored with pop-up satellite archival tags; 10 deployed in the ETA and 37 in the western North Atlantic (WNA). A plot of MDDs encountered, versus dissolved oxygen levels at 100 m, clearly showed that blue marlin ventured deeper when dissolved oxygen levels $>3.5 \text{ ml l}^{-1}$ were available (Fig. 3a). In addition, we illustrate a transition of vertical habitat use by comparing MDDs in the WNA, where ample dissolved oxygen does not limit diving depth, with the ETA, where dissolved oxygen is progressively more limited with depth moving eastward (Fig. 3b–f). Oxygen data shown in Fig. 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 $>200 \text{ m}$ (Fig. 3b,d). In contrast, one blue marlin in the ETA moved northwest, remaining in the upper 100 m while inside the OMZ (Fig. 3c,e), then explored depths $>200 \text{ m}$ 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,f), spending most of its time at depths $\leq 100 \text{ m}$.

Our results revealed that dissolved oxygen 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 dissolved oxygen decrease in the ETA is an ongoing process with local trends of the order of $-0.01 \text{ ml l}^{-1} \text{ yr}^{-1}$ (Supplementary Information). The low dissolved oxygen levels seem to restrict the vertical movement of blue marlin in the habitat-compressed areas, as depicted by the MDDs encountered before and after transiting the OMZ boundary (Fig. 3e). In the WNA, no dissolved oxygen $\leq 3.5 \text{ ml l}^{-1}$ exists in the upper 800 m, allowing greater vertical habitat use (Fig. 3d). In the ETA, where dissolved oxygen levels decrease moving eastward, the maximum depths encountered by blue marlin also decreased, as the fish seem 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, clupeids 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 ecosystem¹⁸ 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 (refs 8,26). For example, the average size of sailfin landed in the ETA and ETP has been consistently larger when compared with 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 productivity²⁷, 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 towards more effective management of fish stocks.

Pelagic fishes generally avoid hypoxic conditions¹³, although at least one exception is the bigeye tuna (*Thunnus obesus*), which has unique blood oxygen-binding characteristics allowing lower dissolved oxygen tolerances than other tropical tunas²⁸. Bigeye tuna often occupy areas below the thermocline in the ETA OMZ during diurnal periods where dissolved oxygen levels are consistently $<3.5 \text{ ml l}^{-1}$, and forage in the prey-abundant surface mixed layer at night. Other predatory species, such as the jumbo squid²⁹ (*Dosidicus gigas*), 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 owing 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 marlin²⁶.

OMZ expansion is evident in all tropical ocean basins and throughout the subarctic Pacific¹⁴, 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 fishes⁹. Many of the targeted and by-catch pelagic species harvested in the OMZ are either fully exploited or overfished²², so any potential fishery impacts related to habitat compression warrant particular attention. As 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 $5.95 \times 10^{13} \text{ m}^3$, 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 (for example, tuna) and by-catch species (for example, 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 ensure that these stocks are not diminished further. The increased vulnerability and overexploitation of tropical pelagic fishes⁹ caught in OMZs raises a particular challenge with regard to the high harvest rates taking place in global fisheries at present³⁰. 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 present 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

As most of the biological literature presents dissolved oxygen in millilitres per litre, instead of micromoles per kilogram, we use the former unit of measure to illustrate dissolved oxygen 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 Fig. S1). To construct the mean 2010 state and trend of dissolved oxygen, vertical high-resolution conductivity, temperature and depth profiles since 1960 are subsampled to 8 dbar intervals, and then all oxygen data are binned in $0.5^\circ \times 0.5^\circ \times 10 \text{ dbar}$ 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 a vertical with 30 dbar radius. As the last step before mapping, an interquartile range (IQR) filter is applied to the dissolved oxygen 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 Fig. 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 the trend and mean state of dissolved oxygen.

Pop-up satellite archival tags 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 MDD presented here are described in more detail in the Supplementary Information.

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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. carried out the oceanographic and biological computations and did the art work. M.V., D.W.R.W., P.B. and 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. L.S., E.D.P. and S.S. are equally contributing first authors.

Additional information

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