

Ocean scale hypoxia-based habitat compression of Atlantic istiophorid billfishes

ERIC D. PRINCE,^{1,*} JIANGANG LUO,² C. PHILLIP GOODYEAR,³ JOHN P. HOOLIHAN,¹ DERKE SNODGRASS,¹ ERIC S. ORBESEN,¹ JOSEPH E. SERAFY,¹ MAURICIO ORTIZ¹ AND MICHAEL J. SCHIRIPA¹

¹National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, FL 33149, USA

²Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Causeway, Miami, FL 33149, USA

³1214 North Lakeshore Drive, Niceville, FL 32578, USA

ABSTRACT

Oxygen minimum zones (OMZs) below near-surface optimums in the eastern tropical seas are among the largest contiguous areas of naturally occurring hypoxia in the world oceans, and are predicted to expand and shoal with global warming. In the eastern tropical Pacific (ETP), the surface mixed layer is defined by a shallow thermocline above a barrier of cold hypoxic water, where dissolved oxygen levels are ≤ 3.5 mL L⁻¹. This thermocline (~25–50 m) constitutes a lower hypoxic habitat boundary for high oxygen demand tropical pelagic billfish and tunas (i.e., habitat compression). To evaluate similar oceanographic conditions found in the eastern tropical Atlantic (ETA), we compared vertical habitat use of 32 sailfish (*Istiophorus platypterus*) and 47 blue marlin (*Makaira nigricans*) monitored with pop-up satellite archival tags in the ETA and western North Atlantic (WNA). Both species spent significantly greater proportions of their time in near-surface waters when inside the ETA than when in the WNA. We contend that the near-surface density of billfish and tunas increases as a consequence of the ETA OMZ, therefore increasing their vulnerability to overexploitation by surface gears. Because the ETA OMZ encompasses nearly all Atlantic equatorial waters, the potential impacts of overexploitation are a concern. Considering the obvious differences in

catchability inside and outside the compression zones, it seems essential to standardize these catch rates separately to minimize inaccuracies in stock assessments for these species. This is especially true in light of global warming, which will likely exacerbate future compression impacts.

Key words: Atlantic hypoxia-based habitat compression, climate change, global warming, oxygen minimum zones, tropical pelagic fishes

INTRODUCTION

Spatial and temporal fluctuations of environmental conditions in the world's oceans influence the vertical and horizontal movement of pelagic fishes (Sharp, 1978; Fonteneau, 1997; Prince and Goodyear, 2006; Bigelow and Maunder, 2007). Adequate population estimates of pelagic fishes are often conditioned on spatial distribution assumptions made during the stock assessment process (Brill, 1994; Brill and Lutcavage, 2001). Increasingly, habitat use preferences and associated physiological limits of pelagic species are used to evaluate their influences on catch per unit effort (CPUE) (Hanamoto, 1987; Hinton and Nakano, 1996; Fonteneau, 1997; Goodyear, 2003; Maunder *et al.*, 2006; Bigelow and Maunder, 2007). Making adjustments for these influences (i.e., CPUE standardization) is essential when using catch rates as indices of relative abundance to infer population stock status (Goodyear, 2003; Hinton and Maunder, 2004). Brill and Lutcavage (2001) expressed a similar viewpoint and maintained that understanding environmental influences on movements and depth distributions of tunas and billfishes is important for improving population assessments. In fact, failure to incorporate environmental influences on the distribution of fishes in the standardization process may result in biased estimates of population benchmarks (Bigelow and Maunder, 2007), potentially leading to different stock status perceptions (ICCAT, 2004).

Oxygen minimum zones (OMZs) below near-surface optimums in the eastern tropical seas are among the largest contiguous areas of naturally occurring hypoxia in the world oceans (Bakun, 1996;

*Correspondence. e-mail: eric.prince@noaa.gov

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Diaz, 2001; Stramma *et al.*, 2008). Development of OMZs is primarily a function of prevailing weather patterns and oceanographic/biological processes. These include winds that parallel the coastline off the west coasts of continents, leading to intense nutrient upwelling, the advection process, the absence of significant mixing at depth, stagnant deep water layers, and the extremely productive surface mixed layer that results in a continuous rain of biological material that deteriorates while sinking into the upwelling water mass (Cushing, 1969; Bakun, 1996; Bakun *et al.*, 1999). All these processes contribute to a narrow surface layer with uniform temperature, shallow thermocline with a steep gradient, and a hypoxic environment below the thermocline, which together characterizes the more or less permanent OMZs (Diaz, 2001; Helly and Levin, 2004).

Hypoxia-based habitat compression, associated with OMZs, has been reported for a variety of marine teleosts, including estuarine and coastal species (Eby and Crowder, 2002), demersal reef fishes in the Gulf of Mexico (Stanley and Wilson, 2004), and many other pelagic and demersal species (see review by Ekau *et al.*, 2009). For example, Ingham *et al.* (1977) reported that surface sightings of schooling skipjack tuna (*Katsuwonus pelamis*) in the eastern Atlantic were greater in areas where the oxycline was shallow. Evans *et al.* (1981) explored this further by comparing catch data with environmental indicators (i.e., temperature and dissolved oxygen) to infer habitat limits and vulnerability to surface fishing gears for skipjack tuna in the equatorial eastern and western Atlantic.

Recently, Prince and Goodyear (2006) presented the first empirical data, based on direct measurement of vertical movement, which showed that OMZs restrict the depth distribution of tropical pelagic blue marlin (*Makaira nigricans*) and sailfish (*Istiophorus platypterus*) in the eastern tropical Pacific (ETP), presumably by compressing their suitable physical habitat into a narrow surface layer. In this case, the surface mixed layer extended downward to a variable boundary defined by a shallow thermocline, often around 25–50 m, above a barrier of cold hypoxic water (Prince and Goodyear, 2006). While hypoxia-based habitat compression is evident in the ETP for tropical pelagic fishes, it is not present in the western North Atlantic (WNA), where dissolved oxygen (DO) is not limited at increasing depths (Prince and Goodyear, 2006). Interestingly, the oceanographic features in the eastern tropical Atlantic (ETA) are similar to those in the ETP; however, empirical evidence of hypoxia-based habitat compression for tropical pelagic fishes in the ETA has not yet been reported.

Dissolved oxygen is an important parameter for understanding the role of oceans in climate change (Stramma *et al.*, 2008). In the current cycle of climate change involving escalated global warming and ocean acidification (ocean absorption of anthropogenic CO₂ emissions), oxygen minimum zones in the tropical oceans are predicted to increase in surface extent, total volume and severity while shoaling closer to the sea surface (Bograd *et al.*, 2008; Rosa and Seibel, 2008; Stramma *et al.*, 2008, 2009). Rosa and Seibel (2008) predicted that the synergism between ocean acidification, global warming, and expansion of OMZs will further reduce the habitat available to major oceanic predators. Clearly, the trophic cascading impacts of these processes and the resultant habitat compression on pelagic and demersal biota need to be determined for the major aquatic communities within each affected area.

Objectives of this paper were: (i) to examine the effect of hypoxia-based habitat compression in the ETA by evaluating empirical data on vertical habitat use of eastern and western Atlantic blue marlin and sailfish using pop-up satellite archival tag (PSAT) technology; and (ii) to describe the unique oceanographic features in the Atlantic oxygen minimum zones that contribute to habitat compression and their relevance to management of pelagic resources.

METHODS

Tag sampling design to monitor habitat of Istiophoridae

We followed the PSAT rigging procedures described by Prince and Goodyear (2006) and Goodyear *et al.* (2008). Billfish handling, in-water tagging procedures, and tagging devices reviewed by Prince *et al.* (2002) were also used. PSATs were attached about 4–5 cm below the dorsal midline by inserting a double-barbed medical-grade nylon anchor between the pterygiophores to a depth just short of protruding from the opposite side of the fish. A conventional streamer tag was also inserted posterior of the PSAT (Prince *et al.*, 2002).

PSATs were programmed for deployment durations ranging from 7 to 120 days. Programming protocols for PSATs are detailed in Prince and Goodyear (2006) and Goodyear *et al.* (2008).

We deployed 79 PSATs on blue marlin and sailfish from 2001 to 2006, primarily from recreational fishing vessels, in both the western and eastern tropical-subtropical Atlantic basins using standard trolling gear with natural bait or high-speed lures (Table 1). All PSAT deployment activities were conducted within

Table 1. Summary of pop-up satellite archival tag information for 46 blue marlin (BUM) and 32 sailfish (SAI) deployed in the western North Atlantic (WNA) and eastern tropical Atlantic (ETA) zones during 2002–2006 including: PSAT number (PTT), species, date deployed, days-at-large (DAL), linear displacement, release zone, release location, and location of first Argos transmission.

No.	PTT	Species	Date deployed	DAL	Displacement (nm)	Release zone	Release location	Location of first transmission
1	40615	SAI	01.19.06	28	353	WNA	24.92°N–80.58°W	30.70°N–79.32°W
2	49033	SAI	12.06.05	7	19	WNA	24.92°N–80.58°W	25.08°N–80.28°W
3	39337	SAI	12.06.05	7	203	WNA	24.97°N–80.52°W	28.34°N–80.21°W
4	57189	SAI	05.03.05	6	473	WNA	25.35°N–80.12°W	32.73°N–76.93°W
5	57188	SAI	05.03.05	5	213	WNA	25.34°N–80.14°W	28.88°N–79.98°W
6	57184	SAI	05.10.05	120	157	WNA	24.79°N–84.55°W	24.46°N–81.70°W
7	57183	SAI	05.08.05	6	2	WNA	24.46°N–81.75°W	24.48°N–81.72°W
8	57182	SAI	05.08.05	120	868	WNA	24.44°N–81.80°W	36.33°N–72.21°W
9	57181	SAI	05.08.05	118	123	WNA	24.45°N–81.76°W	25.70°N–79.97°W
10	57180	SAI	05.03.05	120	757	WNA	24.46°N–81.69°W	27.64°N–95.28°W
11	57179	SAI	05.11.05	135	129	WNA	24.49°N–81.54°W	26.10°N–79.95°W
12	57178	SAI	04.28.05	119	225	WNA	24.43°N–81.89°W	27.84°N–80.17°W
13	57177	SAI	05.11.05	119	241	WNA	24.50°N–81.55°W	27.45°N–78.51°W
14	57176	SAI	04.25.05	118	569	WNA	24.43°N–81.92°W	33.44°N–78.55°W
15	42721	SAI	01.23.04	52	78	WNA	25.68°N–80.08°W	26.98°N–80.05°W
16	40606	SAI	04.30.03	62	354	WNA	25.70°N–80.17°W	26.60°N–73.67°W
17	33177	SAI	04.09.03	13	351	WNA	25.69°N–80.09°W	31.53°N–79.62°W
18	33176	SAI	04.09.03	8	70	WNA	25.82°N–80.11°W	24.78°N–80.70°W
19	39335	SAI	03.03.03	8	107	WNA	25.83°N–80.08°W	27.60°N–79.93°W
20	39334	SAI	04.03.03	8	93	WNA	25.75°N–80.29°W	26.73°N–78.96°W
21	66699	SAI	06.28.06	114	206	ETA	14.08°N–17.18°W	10.67°N–17.54°W
22	66700	SAI	06.26.06	90	46	ETA	14.05°N–17.18°W	13.46°N–17.68°W
23	66703	SAI	07.02.06	90	160	ETA	14.46°N–17.25°W	12.01°N–18.34°W
24	66704	SAI	07.02.06	116	28	ETA	14.45°N–17.27°W	13.99°N–17.19°W
25	66705	SAI	07.02.06	90	205	ETA	14.44°N–17.28°W	11.03°N–17.27°W
26	66707	SAI	07.02.06	21	11	ETA	14.44°N–17.24°W	14.41°N–17.06°W
27	66708	SAI	07.03.06	145	87	ETA	14.45°N–17.25°W	13.44°N–18.33°W
28	57197	SAI	07.04.05	5	33	ETA	14.51°N–17.37°W	13.98°N–17.21°W
29	57199	SAI	07.05.05	46	23	ETA	14.59°N–17.41°W	14.23°N–17.30°W
30	57201	SAI	07.07.05	95	1050	ETA	14.42°W–17.33°W	01.76°N–05.11°W
31	57204	SAI	07.08.05	3	17	ETA	14.60°N–17.32°W	14.36°N–17.18°W
32	57196	SAI	07.04.05	60	67	ETA	14.51°N–17.36°W	13.39°N–17.43°W
33	49773	BUM	05.09.04	21	154	ETA	16.98°N–25.35°W	14.43°N–25.57°W
34	49774	BUM	05.10.04	47	756	ETA	16.92°N–25.33°W	28.41°N–30.95°W
35	49775	BUM	05.12.04	70	393	ETA	16.75°N–25.10°W	17.42°N–18.28°W
36	49777	BUM	05.10.04	15	371	ETA	16.95°N–25.38°W	13.45°N–30.66°W
37	49778	BUM	05.12.04	56	161	ETA	16.75°N–25.10°W	17.68°N–22.47°W
38	53244	BUM	10.16.04	44	924	ETA	07.85°S–14.40°W	07.37°N–16.78°W
39	53245	BUM	10.19.04	36	390	ETA	07.90°S–14.23°W	02.85°S–10.11°W
40	53733	BUM	10.14.04	4	15	ETA	07.90°S–14.43°W	08.10°S–14.57°W
41	53734	BUM	11.17.04	38	347	ETA	07.90°S–14.43°W	03.54°N–10.60°W
42	53736	BUM	11.07.04	90	1373	ETA	07.00°S–14.00°W	26.78°S–26.10°W
43	41535	BUM	09.02.03	28	263	WNA	18.57°N–66.22°W	14.59°N–64.29°W
44	41540	BUM	09.03.03	7	57	WNA	18.57°N–66.22°W	19.06°N–65.36°W
45	42723	BUM	09.03.03	124	1397	WNA	18.53°N–66.18°W	03.08°N–48.39°W
46	42724	BUM	09.03.03	115	163	WNA	18.53°N–66.18°W	18.63°N–63.32°W
47	42722	BUM	09.03.03	39	1477	WNA	18.57°N–66.22°W	05.17°N–45.06°W
48	23388	BUM	06.07.03	60	428	WNA	20.26°N–72.47°W	16.23°N–66.27°W
49	23389	BUM	06.08.03	61	406	WNA	20.25°N–72.83°W	16.02°N–67.27°W

Table 1. (Continued).

No.	PTT	Species	Date deployed	DAL	Displacement (nm)	Release zone	Release location	Location of first transmission
50	23397	BUM	06.09.03	38	80	WNA	20.30°N–72.62°W	18.98°N–72.85°W
51	41537	BUM	07.24.03	45	498	WNA	32.13°N–65.01°W	36.11°N–56.20°W
52	41527	BUM	07.14.03	41	203	WNA	32.05°N–65.03°W	34.78°N–67.43°W
53	41516	BUM	06.11.03	57	212	WNA	24.05°N–75.43°W	27.25°N–73.78°W
54	41518	BUM	06.05.03	63	492	WNA	24.33°N–72.53°W	31.20°N–77.59°W
55	41520	BUM	06.05.03	63	825	WNA	24.10°N–75.25°W	36.85°N–69.23°W
56	41521	BUM	06.07.03	61	176	WNA	24.10°N–75.25°W	22.25°N–72.77°W
57	41522	BUM	06.09.03	10	80	WNA	24.08°N–75.25°W	24.98°N–74.17°W
58	41523	BUM	06.04.03	95	218	WNA	24.10°N–75.25°W	24.55°N–71.29°W
59	41524	BUM	06.04.03	82	319	WNA	24.10°N–75.28°W	19.03°N–73.56°W
60	41525	BUM	06.07.03	41	342	WNA	24.12°N–75.27°W	29.79°N–75.85°W
61	41526	BUM	06.07.03	84	699	WNA	24.12°N–75.30°W	35.70°N–73.83°W
62	41528	BUM	06.10.03	69	255	WNA	24.11°N–75.28°W	28.26°N–74.28°W
63	41530	BUM	06.26.03	7	91	WNA	22.85°N–74.41°W	24.36°N–74.42°W
64	41531	BUM	06.19.03	91	199	WNA	22.00°N–72.06°W	23.93°N–69.12°W
65	41534	BUM	06.17.03	46	549	WNA	22.00°N–72.07°W	19.13°N–62.78°W
66	41538	BUM	06.16.03	47	1125	WNA	21.99°N–72.03°W	14.29°N–54.01°W
67	41539	BUM	06.18.03	74	92	WNA	21.99°N–72.06°W	20.62°N–71.31°W
68	25999	BUM	06.14.02	45	747	WNA	23.93°N–74.59°W	17.41°N–63.24°W
69	22872	BUM	06.14.02	28	353	WNA	23.94°N–74.61°W	25.00°N–68.26°W
70	23077	BUM	06.21.02	19	71	WNA	23.79°N–74.36°W	24.93°N–74.70°W
71	26001	BUM	07.08.02	25	795	WNA	22.78°N–74.39°W	35.51°N–70.16°W
72	26005	BUM	07.06.02	13	72	WNA	22.82°N–74.38°W	22.70°N–75.68°W
73	23520	BUM	07.02.02	25	245	WNA	22.80°N–74.35°W	26.79°N–73.41°W
74	27825	BUM	10.12.02	29	566	WNA	18.71°N–64.82°W	15.56°N–74.13°W
75	22870	BUM	06.09.02	36	499	WNA	28.71°N–78.89°W	36.27°N–74.76°W
76	23548	BUM	06.11.02	33	490	WNA	28.76°N–78.79°W	35.99°N–74.37°W
77	26935	BUM	10.12.02	39	287	WNA	18.72°N–64.83°W	21.78°N–60.92°W
78	23205	BUM	10.13.02	38	1193	WNA	18.72°N–64.82°W	07.54°N–47.90°W
79	39334	BUM	10.14.02	43	229	WNA	18.85°N–64.79°W	22.44°N–66.18°W

50 miles of the coastlines off South Florida, the Bahamas, Turks and Caicos Islands and U.S. Virgin Islands in the WNA, and off Cape Verde Islands, Ascension Island, and Dakar, Senegal, in the ETA (Fig. 1). Wildlife Computers¹ (Redmond, WA) PAT4 and Mk10 were the primary PSAT models used, although a few PAT2 and PAT3 models were used during 2001–2003. The PSATs were programmed to sample depth (pressure), temperature and light once every 30 or 60 s. The depth and temperature records for a few of the early deployments were summarized by the software on-board the tag into histograms at 3-h intervals, but the vast majority of the data were compiled by the on-board software into histograms at

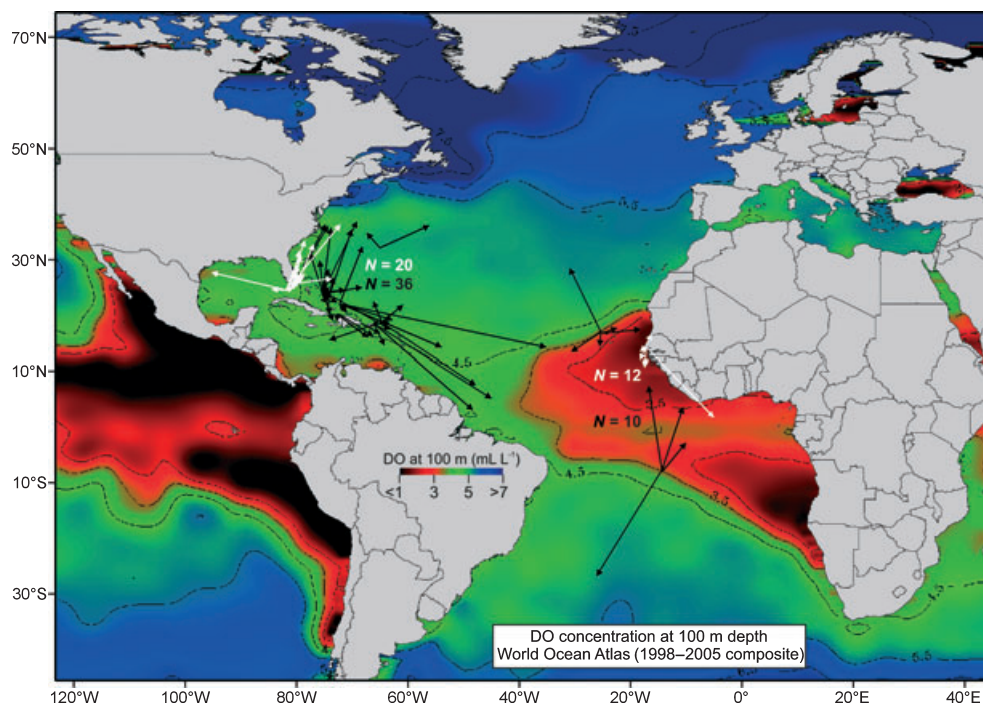
6-h bin intervals. We programmed the tag to summarize temperature bins starting at <12°C, then each successive 2°C interval ending with >32°C. Likewise, depth bins started at <–1 m, then successive intervals of 25 m until ending at depths >250 m. The aggregate mean proportions for monitoring time and records with one or more dives (to the maximum depth recorded in a record) were calculated within <50, >50, >100, and >200-m depth strata, then compared among species/area treatments.

Statistical analysis of vertical habitat use

General linear model (GLM) univariate procedures in SPSS software (Chicago, IL, USA) were used to compare group mean proportions (arcsine transformed data) for aggregate time spent at-depth and maximum dive records between the ETA and WNA. Maximum dive records were extracted from individual 6-h summary bins. For analytical purposes, data were assigned

¹References to commercial products do not imply endorsement by the National Marine Fisheries Service or the authors.

Figure 1. Displacement vectors and number of deployments for blue marlin (*Makaira nigricans*, black lines/arrows) and sailfish (*Istiophorus platypterus*, white lines/arrows) tagged with pop-up satellite archival tag (PSAT) technology in the western North Atlantic (WNA) and eastern tropical Atlantic (ETA). Annual mean dissolved oxygen (DO, mL L^{-1}) concentrations at 100-m depths are from the World Ocean Atlas (1998–2005).



to four arbitrary depth strata (0–50 m, 51–100 m, 101–200 m, and >200 m). In the evaluation, area (i.e., ETA or WNA) was used as a fixed variable, depth as a random variable, and proportion of time at-depth (or maximum dives) as the dependent variable. Light level derived geolocations allowed estimation of dates when two blue marlin (PTT 49774 and 53736) tagged in the ETA OMZ moved outside this area. Data for these two individuals were split to correspond with the time and area of occupancy. Computations for mean maximum dives per day and mean temperature for these maximum dives both inside and outside ETA used the same statistical approach as the aggregate analysis.

Oceanography of the study areas

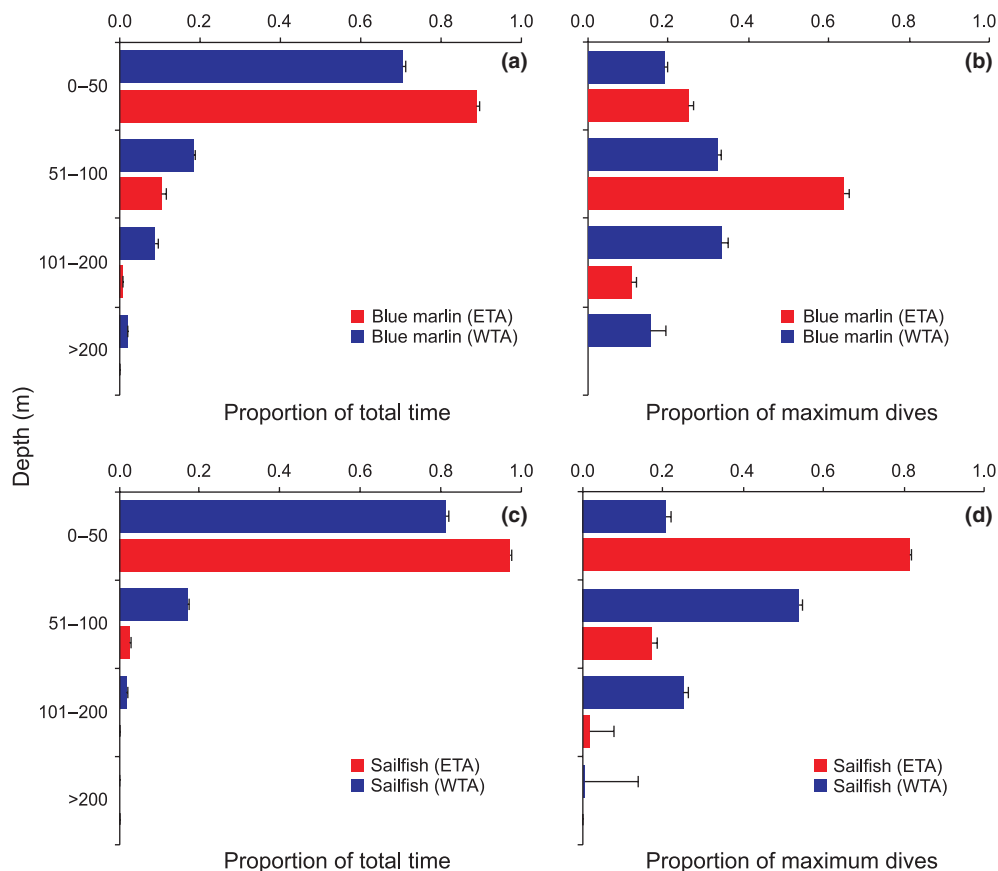
We constructed distributions of temperature, DO, and salinity at-depth profiles in the rectangles given by the co-ordinates of the PSAT deployment and pop-off locations for each month at-large for individual fish pooled by ETA or WNA study areas. These compilations employed the objectively analyzed monthly means for each variable at 1° of latitude and longitude from the World Ocean Atlas 2005 (WOA05) (<http://www.nodc.noaa.gov/OC5/WOA05/woa05data.html>,

Antonov *et al.*, 2006; Locarnini *et al.*, 2006; Garcia *et al.*, 2006). Vertical profiles of temperature ($^\circ\text{C}$), DO (mL L^{-1}), and salinity (psu) were constructed as annual mean values for both ETA and WNA zones with dispersion of ± 1 SD to represent estimated oceanographic features likely encountered by our tagged animals. The spatial distributions of the DO concentration at 100-m depth are either annual mean values (for general purpose) or seasonal values (to match the season of tag deployment). We adopted the DO threshold of 3.5 mL L^{-1} from Prince and Goodyear (2006) based on lethal levels of DO reported for tropical pelagic fishes, as well as DO levels that induce symptoms of stress in these species (Ingham *et al.*, 1977; Evans *et al.*, 1981; Gooding *et al.*, 1981; Bushnell and Brill, 1991; Post *et al.*, 1997; Idrisi *et al.*, 2002). For the purposes of this study, we define the ETP and ETA as OMZs exhibiting DO levels of $\leq 3.5 \text{ mL L}^{-1}$ at 100-m depths (Fig. 1).

Use of the Kalman filter for horizontal tracks

Fish movement tracks were derived from light-level, temperature, and bathymetric data. Light-level geolocation data were initially processed using the global positioning software WC-AMP (Wildlife Computers,

Figure 2. Proportions of vertical activity for blue marlin and sailfish PSAT tagged in the western North Atlantic (WNA) and eastern tropical Atlantic (ETA). (a) Blue marlin, time at-depth. (b) Blue marlin, maximum dives. (c) Sailfish, time at-depth. (d) Sailfish, maximum dives. ETA is designated by red and WNA by blue. Y-bars = $2 \times \text{SE}$.



Redmond, WA, USA), and then applying a sea-surface temperature-corrected Kalman filter (Nielsen *et al.*, 2006) to the light level-derived locations. These sea surface temperature-corrected geolocations have a reported accuracy of ≤ 111 km (Nielsen *et al.*, 2006). Finally, we used a custom bathymetry filter to relocate the points that were on land or in shallow water, based on 2×2 min grid ETOP02 bathymetry data (Anon, 2006) and the daily maximum depth from the PSAT (Hoolihan and Luo, 2007).

RESULTS

Vertical habitat use of billfishes

A total of 79 PSATs were deployed on blue marlin and sailfish in the WNA and ETA from 2001 to 2006 (Fig. 1; Table 1). Blue marlin were monitored for an aggregate 410 days (10 PSATs) in the ETA and 1283 days (36 PSATs) in the WNA, whereas sailfish were monitored for an aggregate 932 days (12 PSATs)

in the ETA and 1161 days (20 PSATs) in the WNA (Table 1).

The mean proportion of monitoring time (0.88, SD 0.15) spent in the 0–50-m depth stratum for ETA blue marlin was significantly greater ($P < 0.001$) compared to the proportion (0.71, SD 0.28) for WNA blue marlin (Fig. 2a). In comparison, the proportions of time spent in the three deeper depth strata were all significantly greater ($P < 0.01$) for WTA blue marlin (Fig. 2a).

Using the maximum dive records from the 6-h bin intervals, a pairwise comparison of the mean differences between the ETA and WNA blue marlin showed a significantly greater number of maximum dives ending in the 0–50 m ($P = 0.011$) and 51–100 m ($P = 0.000$) strata for the ETA blue marlin (Fig. 2b). In contrast, the mean differences for maximum dives to the 101–200 and >200 m strata were significantly greater ($P < 0.001$) for WNA blue marlin (Fig. 2b). No blue marlin in the ETA descended >200 m, whereas 30 (83%) of WNA individuals did (Fig. 2b).

The mean proportion of total time at-depth in the 0–50 m stratum by sailfish in the ETA (0.97) was significantly greater ($P < 0.001$) than the WNA (0.81, Fig. 2c). In contrast, time at-depth in the 51–100 m stratum was significantly greater in the WNA (0.16), compared to the ETA (0.02, Fig. 2c). Time at-depth below this stratum was negligible, particularly for the ETA group (Fig. 2c).

Sailfish in the ETA exhibited a significantly greater ($P < 0.001$) mean number of maximum dives ending in the 0–50 m stratum (Fig. 2d), whereas WNA sailfish showed significantly higher means ($P < 0.001$) for maximum dives in the 51–100 and 101–200 m strata (Fig. 2d). Only one of 12 (8.3%) ETA sailfish descended >200 m, as compared to five of 20 (25%) WNA individuals.

Billfish movement across the WNA/ETA boundaries

During the study period, two blue marlin, PTT 49774 and 53736 (Table 1), released in the ETA undertook movements leading outside the OMZ (Figs 3a–c and 4a–c). These marlin were at-large 47 days and 90 days and had displacement distances of about 1400 and 2543 km, respectively (Figs 3a and 4a). Kalman filter tracks of these marlin allowed estimation of the dates where transboundary movements between the ETA and waters outside this area were made, which in turn allowed analysis of vertical habitat use by the same fish inside and outside the OMZ (shown in red/black in Figs 3a–c and 4a–c). We compared maximum daily depth records, and estimated temperature at those depths for PTT 49774 and 53736 (Figs 3a–c, and 4a–c), for activity inside and outside the ETA. For PTT 49774, the mean daily maximum depth reached inside the ETA was 91 m (SD 26) compared to 205 m (SD 89) outside. Mean daily temperatures estimated at these maximum depths inside the ETA were 21°C (SD 2) compared to 21°C (SD 3) outside. For PTT 53736, the mean daily maximum depth reached inside the ETA was 98 m (SD 51) compared to 189 m (SD 56) outside. The mean temperatures estimated at these maximum daily depths inside the ETA were 21°C (SD 5) compared to 18°C (SD 3) outside. Both blue marlin explored maximum daily depths and associated lower water temperatures outside the ETA that were significantly greater ($P < 0.000$) than those inside the ETA.

Oceanographic conditions in the WNA and ETA

The temperature, DO, and salinity levels that our tagged animals likely encountered in the two Atlantic study areas are shown in Fig. 5. Of these, the greatest disparity between study areas was clearly the differences in DO profiles (Fig. 5a). The DO concentrations

in the ETA were $\leq 3.5 \text{ mL L}^{-1}$ below the thermocline (25–50-m depth strata), whereas in the WNA, DO levels were maintained above this level through 400-m depths, then tailed off gently to 3.2 mL L^{-1} through 800-m depths. The DO gradient in the ETA was most severe between 10 and 50 m and then became more moderate at depths below 75 m. There was a slight DO increase in the ETA after 600 m through the deepest depth strata shown (800 m), from 1.5 to 2.2 mL L^{-1} , respectively. In the WNA, DO was above the 3.5 mL L^{-1} threshold for the first 300 m, then varied between 3.2 and 3.5 mL L^{-1} thereafter. After the first 10 m, DO in the WNA was always higher than the ETA. Patterns for the temperature and salinity profiles for the WNA and ETA were less pronounced, though similar, to the DO patterns (Fig. 5b,c).

DISCUSSION

For decades, OMZs have been reported to occur as distinct strata in large equatorial regions of the eastern tropical Pacific and Atlantic Oceans (Sund *et al.*, 1981; Bakun, 1996; and Helly and Levin, 2004). While comparisons of skipjack tuna sightings and catch data to environmental indicators (i.e., temperature and DO) have suggested vertical habitat compression within these OMZs (Evans *et al.*, 1981), only recently have empirical data (Prince and Goodyear, 2006) demonstrated this phenomenon for high oxygen-demand blue marlin and sailfish (Post *et al.*, 1997; Wegner *et al.*, 2010). These data suggested that suitable physical habitat of the ETP was compressed into a narrow surface mixed layer, and the cold hypoxic environment below the thermocline limited vertical habitat use for tropical pelagic fishes (Prince and Goodyear, 2006).

Prince and Goodyear (2006) reported that the preferred prey of marlin and sailfish (e.g., clupeids, carangids, small tunas), which are also obligate ram ventilators, would be restricted to the same narrow surface mixed layer. They suggested this would lead to increased interaction between predator and prey, providing enhanced foraging opportunities for the predators, thus attracting predators to these compression zones. Historical data (1958–2005) from the International Commission for the Conservation of Atlantic Tunas (ICCAT) and Inter-American Tropical Tuna Commission (IATTC) indicate a larger average size for sailfish landed in the ETP and ETA compared to the WNA [about 184 cm lower jaw fork length (LJFL) versus 164 cm LJFL, respectively], which may reflect these increased foraging opportunities (Prince and Goodyear, 2006).

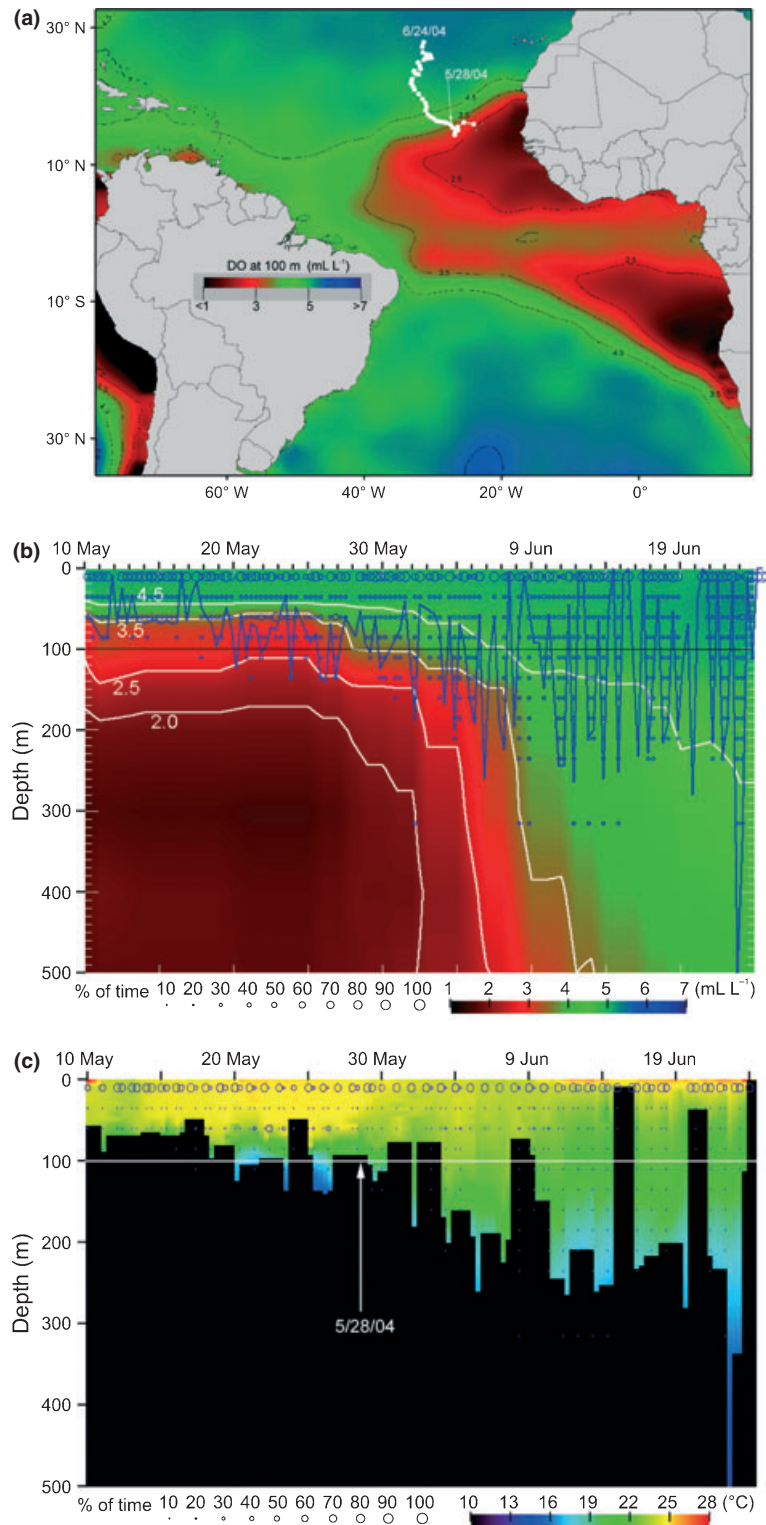


Figure 3. (a) Kalman filter track (shown in white, see Methods) of a blue marlin (*Makaira nigricans*, PTT 49774) PSAT deployment initially released in the ETA that made a transboundary movement outside the ETA. The dates of transboundary crossing between study areas (28 May 2004) and the end point of PSAT transmission (24 June 2004) are identified. (b) Spring mean level of dissolved oxygen at depth estimated from the World Ocean Atlas (1998–2005) for maximum dives (shown as blue line) during the track (PTT 49774). Percent time at DO/maximum depth is proportional to the size of blue ovals. (c) Spring mean temperature at depth estimated from the World Ocean Atlas (1998–2005) for maximum dives during the track (49774). Percent time at temperature/maximum depth is proportional to the size of black ovals.

The aggregate monitoring time achieved in the present study was well over 1 yr for each of the species/area treatments and are in general agreement with findings reported for the ETP (Prince and

Goodyear, 2006). We have presented empirical data on vertical habitat use of Atlantic istiophorid billfish and the associated oceanographic conditions they likely encountered in the WNA versus ETA

Figure 4. (a) Kalman filter track (shown in white, see Methods) of a blue marlin (*Makaira nigricans*, PTT 53736) PSAT deployment initially released in the ETA that made a transboundary movement outside the ETA. The dates of transboundary crossing between study areas (21 December 2004) and the end point of PSAT transmission (5 February 2005) are identified. (b) Winter mean level of dissolved oxygen at depth estimated from the World Ocean Atlas (1998–2005) for maximum dives (shown as blue line) during the track (PTT 53736). Percent time at DO/maximum depth is proportional to the size of blue ovals. (c) Winter mean temperature at depth estimated from the World Ocean Atlas (1998–2005) for maximum dives during the track (53736). Percent time at temperature/maximum depth is proportional to the size of black ovals.

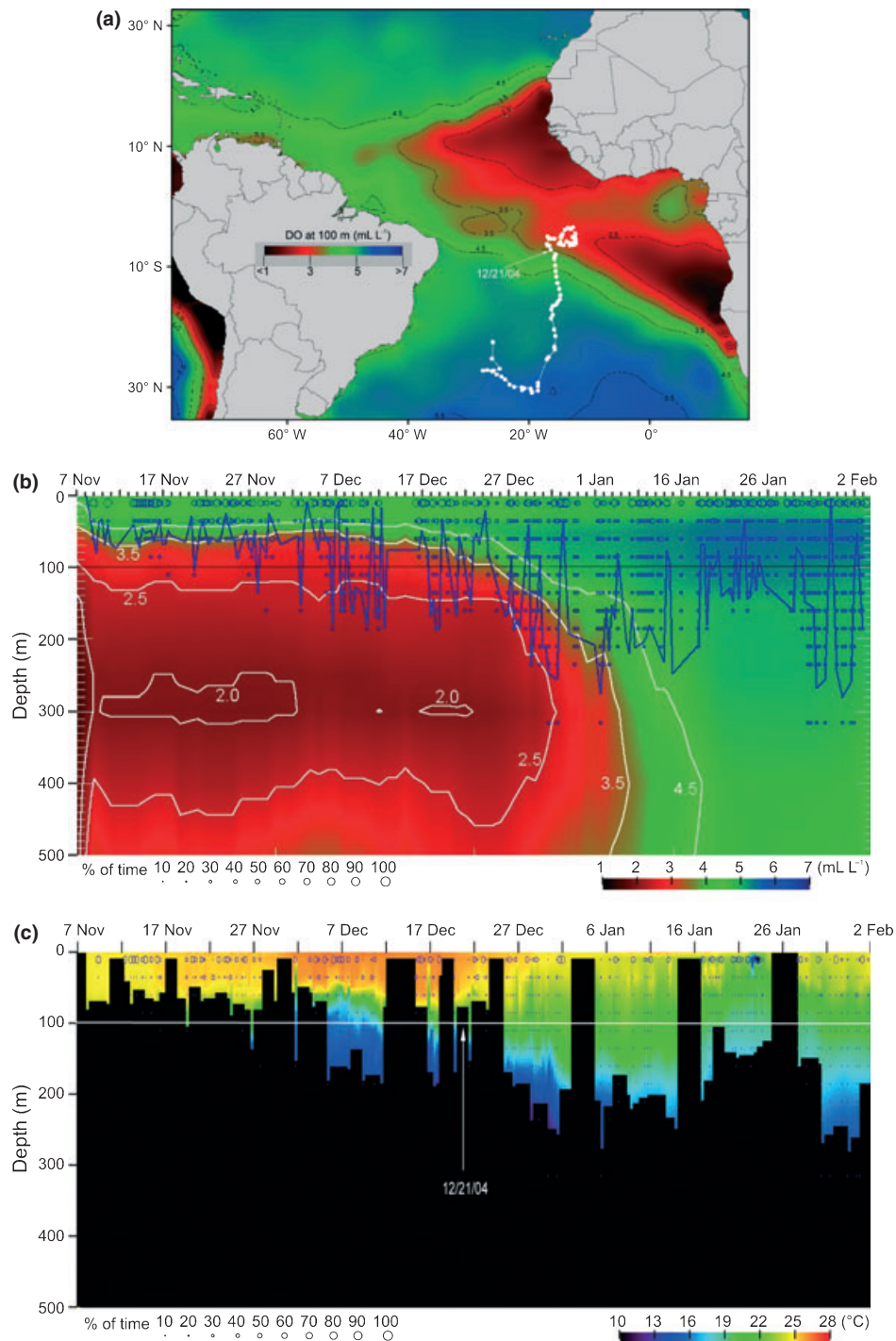
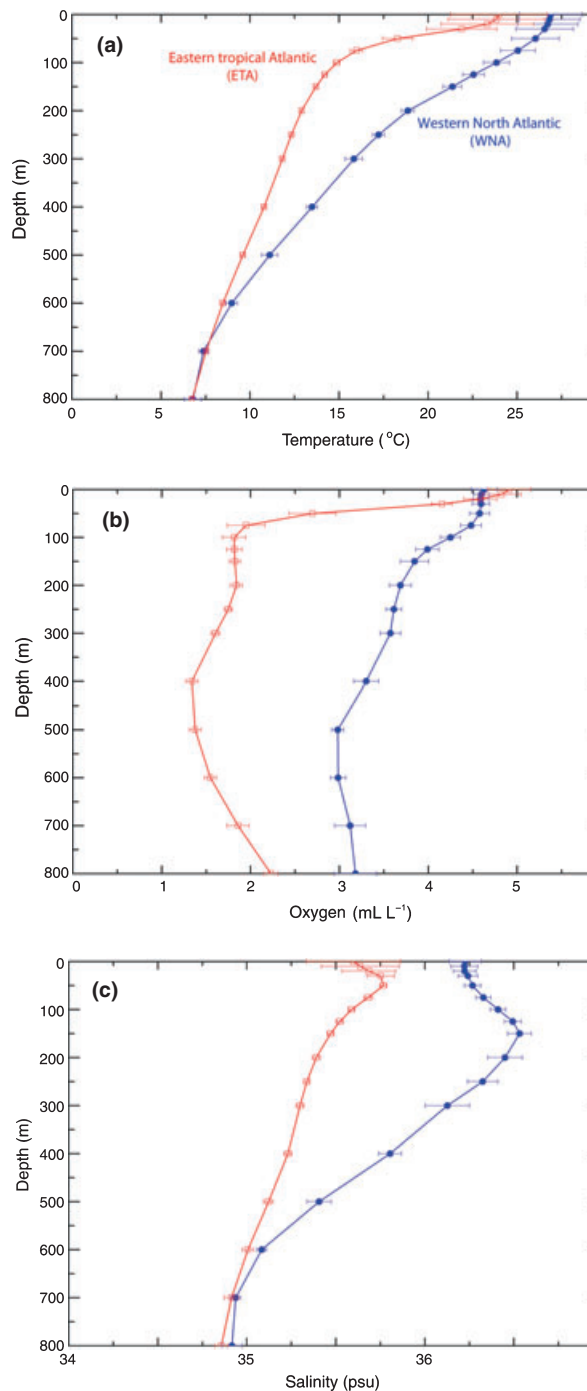


Figure 5. Temperature [$^{\circ}\text{C}$ (a)], dissolved oxygen [DO , mL L^{-1} (b)], and salinity [psu (c)] profiles derived from the 1998–2005 World Ocean Atlas data for the western North Atlantic (WNA, blue) and the eastern tropical Atlantic (ETA, red). Temperature, DO, and salinity data are annual means and horizontal error bars are ± 1 SD.



(Figs. 2–5). Our aggregate analysis of vertical habitat use of blue marlin and sailfish, based on monitoring time at depth and maximum dives (Fig. 2a–d),

clearly showed a significant increased use of the near-surface depths by both species while in the ETA versus the WNA. Conversely, both marlin and sailfish exhibited much greater use of the deeper depth strata while in the WNA. For example, in the ETA only one sailfish descended below the 200-m depth strata, whereas no blue marlin descended below this level. Alternatively, in the WNA, five (25%) sailfish and 36 (83%) blue marlin descended below 200 m. There were also species-specific trends that were consistent in both study areas. Sailfish demonstrated more extensive use of the surface mixed layer and less use of the deeper depth strata compared to the much larger blue marlin, no matter which study area they were tagged in.

Trends in aggregate vertical habitat analysis and associated oceanographic conditions were further reinforced by the vertical habitat behavior of two blue marlin that were tagged inside the ETA and eventually moved outside this zone (Figs 3a–c and 4a–c). The daily maximum dives inside and outside the compression area (ETA) closely correspond to the trends illustrated in the aggregate analysis (i.e., much greater use of the vertical habitat while outside the OMZ). In addition, mean maximum depth and mean temperature at depth for maximum dives provided a high resolution view depicting the markedly different habitat use of the same fish inside and outside of the ETA (Figs 3 and 4). It is also clear that blue marlin may be capable of making very short-term maximum (spike) dives to strata below the 3.5 mL L^{-1} DO threshold (Figs 3b and 4b); long-term survival at these levels would not be sustainable (Brill, 1994). Short forays into DO strata below 3.5 mL L^{-1} are not surprising given the rapidly decreasing DO at-depth gradients in the ETA, where DO can decrease in only a few meters (Fig. 5). Thus, this DO threshold should not be interpreted as an absolute barrier, as the behavior of the blue marlin that moved out of the OMZ demonstrated (Figs 3c and 4c). All tropical pelagic fishes require obligate ram ventilation to sustain respiratory function and support their very high metabolic rates (Roberts, 1978; Brill, 1996). In addition, these species share similarly high metabolic characteristics (Brill, 1996) and react to hypoxic conditions primarily by avoidance (Randall, 1970).

Our data confirm that the oceanographic phenomenon of hypoxia-based habitat compression clearly exists in the ETA for tropical pelagic fishes. These findings support those reported by Prince and Goodyear (2006), who documented the compression phenomena for tropical pelagic fishes in the ETP. Moreover, Prince and Goodyear (2006) concluded

that 'the shallow band of acceptable habitat restricts these fishes to a very narrow surface layer and makes them more vulnerable to overexploitation by surface gears'. Thus, increased exposure and vulnerability of tropical pelagic fishes to overexploitation by surface gears is also a major concern for the ETA.

Oxygen minimum zones in the ETA and ETP

Although the oceanographic features of the ETA are similar to those found in the ETP, the compression zones in both equatorial regions, based on 3.5 mL L^{-1} DO threshold at 100 m, are quite different (Fig. 6). The ETP has about 55% more surface area ($23.37 \times 10^6 \text{ km}^2$ versus $13 \times 10^6 \text{ km}^2$) and extends westward about twice the distance of the ETA (8065 km versus 5134 km, respectively). Although both compression areas have the most severe hypoxia (about 0.5 mL L^{-1}) nearest their continental coastlines (represented by the black shading in Fig. 6), this area is also much larger and appears more severe in the ETP. A common feature of the ETP and ETA is the apparent moderation of hypoxia at the equator, which presents a bimodal appearance. This is likely an effect of equatorial counter currents between northern and southern gyres (Fig. 6).

The ETA OMZ represents about 16% of ICCAT jurisdictional waters inhabited by tropical pelagic fishes (Fig. 7). Despite being about half the size and having moderately higher DO levels at 100 m than the ETP, the ETA OMZ's extensive geographical coverage of the tropical Atlantic results in a dominant oceanographic feature in terms of potential fishery impacts and management concerns for the affected species. For example, the importance of the ETA to ICCAT tropical tuna management is illustrated by the fact that more than 75% of the historical purse seine landings of yellowfin tuna (*Thunnus albacares*) (Fig. 7) are caught in the ETA OMZ (which is only 16% of ICCAT jurisdictional waters for this species). Moreover, about 90% of the conventional tag recoveries of yellowfin tuna that made transatlantic crossings were in the ETA, illustrating the connectivity in between the WNA and ETA (Fig. 7). The compression impacts and associated limited use of vertical habitat apply equally to both high oxygen demand yellowfin tuna and billfish in the ETA OMZ, as they share a similar gill morphology, high performance physiology, obligate ram ventilation mode of respiration, and DO tolerances (Brill, 1996; Wegner et al., 2010). In addition, the western edge of the ETA can extend to within 274 km of the eastern edge of Brazil. Thus, the

Figure 6. The compressed area off the eastern tropical Pacific (ETP) and eastern tropical Atlantic (ETA) at 100-m depths. Annual mean dissolved oxygen (DO) levels at 100-m depths are in mL L^{-1} from the World Ocean Atlas website. The lower DO threshold for tropical pelagic species (adopted from Prince and Goodyear, 2006) are $\leq 3.5 \text{ mL L}^{-1}$ (shown in red/black).

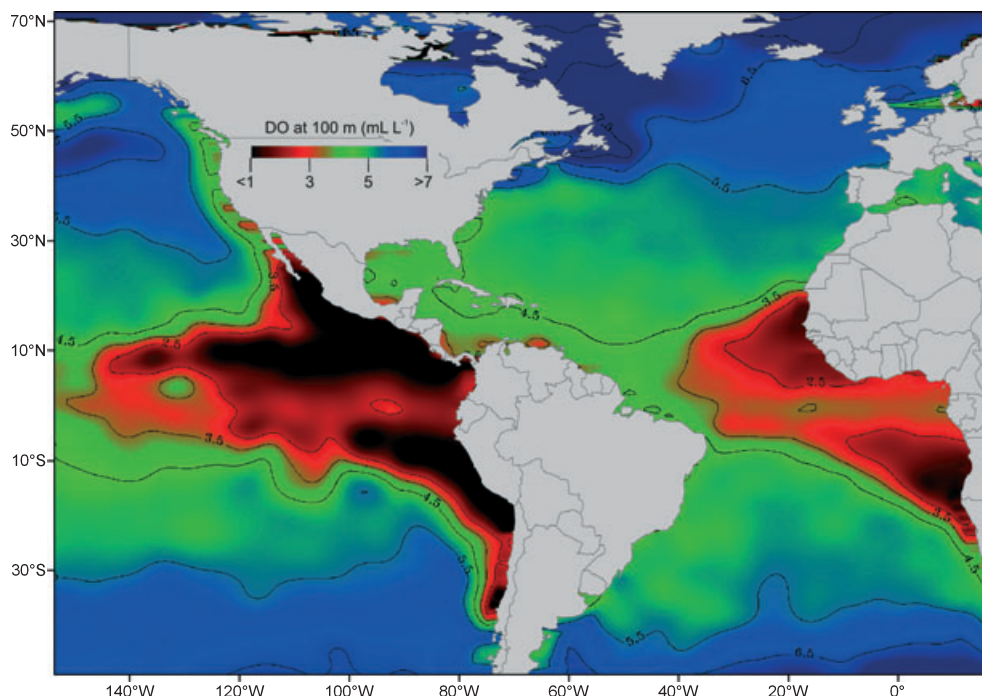


Figure 7. We derived the size of the surface area ($12.99 \times 10^6 \text{ km}^2$) of the compression zone off West Africa based on the annual mean dissolved oxygen levels at 100-m depths from the World Ocean Atlas 1998–2005 composite. This area represents about 16% of the total Atlantic ICCAT jurisdictional waters for tropical pelagic billfish and tunas (represented as the area between red dashed horizontal lines in the North and South Atlantic). Historical purse seine landings of yellowfin tuna (*Thunnus albacares*) from the International Commission for the Conservation of Atlantic tunas (ICCAT), 1958–2005. Size of yellow circles is proportional to metric tons. Displacement vectors (white lines/arrows) indicates transatlantic movements of yellowfin tuna tagged in the U.S. western North Atlantic with conventional tags and recovered inside the compressed area off West Africa (tropical eastern Atlantic).

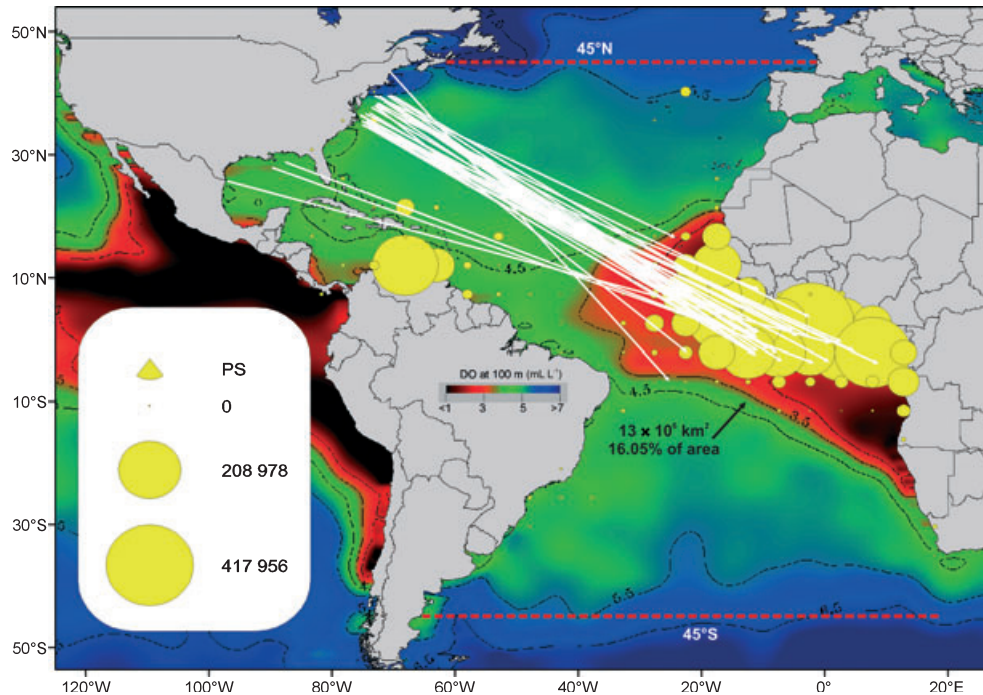
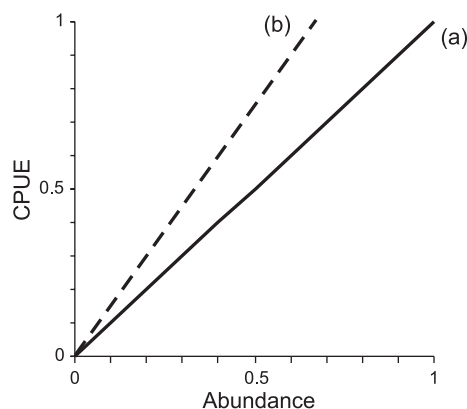


Figure 8. The hypothesized relationship between catch per unit effort (CPUE) and abundance for tropical pelagic billfish and tuna in uncompressed (a) and compressed (b) environments (e.g., hypoxia-based habitat compression via oxygen minimum zones).



ETA 3.5 mL L^{-1} oxycline at 100 m covers nearly all equatorial Atlantic waters. This is not the case for the ETP (Fig. 6), a consequence likely due to the disparity

in size of the two ocean basins (Pacific being much larger).

Compression impacts and the stock assessment process

Because habitat compression effectively increases fish concentrations near the surface, the rate at which fish are caught as a result of one unit of effort will be different for the same gear when it is fished inside versus outside the compressed area. In other words, compressed habitat will have a higher density of tropical pelagic predators and their preferred prey per cubic meter of water. This, in turn, presents implications when using catch per unit effort as an index of relative abundance. For example, with longline fishing gear, most of the hooks are distributed shallower than 100 m due to the catenary geometry of the longline (Rice *et al.*, 2007). In compressed habitat, the hook and fish encounter rate will increase significantly as fish distributions are compressed to the 100 m surface layer as compared to the distribution (0–300 +m) in uncompressed habitat.

Two possible hypothesized relationships between CPUE and abundance are illustrated in Fig. 8. Line (a)

depicts the relationship in an uncompressed habitat, and line (b) the relationship in an area of habitat compression. Both illustrate the assumed proportional relationship between CPUE and relative abundance (Fig. 8). These trends are consistent with purse seine experiments showing elevated catch rates and increased vulnerability of tropical tunas inside ETP and ETA OMZs, compared to outside these areas (Murphy and Niska, 1953; Brock, 1959; Green, 1967; Sharp, 1978; Evans *et al.*, 1981; Sund *et al.*, 1981). In other words, at an equivalent level of abundance, the CPUE in the compressed area will be higher than that of the uncompressed habitat simply due to the differences in sampled density (Fig. 8). If data from the two habitat types are inappropriately combined into one estimate of CPUE for the entire area, it will lead to an inaccurate estimate of catchability and, subsequently, inaccurate historic estimations of the index of relative abundance of the stock. Furthermore, the resulting index of relative abundance would be even more inaccurate to the stock assessment result if the OMZs were to expand and shoal closer to the surface over time (Stramma *et al.*, 2008). However, if the CPUE data is partitioned by the two different habitat types and a separate catchability can be reasonably assumed or estimated for each, the inaccuracy can be minimized. This suggests that CPUE standardization of data from the same fishery/gear/target from inside and outside a compression area should be handled separately.

If these relationships between CPUE and oceanography (Fig. 8) are confirmed, it would be important to develop separate indices of relative abundance for each habitat, particularly if the exploitation patterns are different. If the assessment model structure can replicate the spatial structure of the habitats, then separate or spatially interpreted indices can and should be applied to each area/habitat. There are already several assessment models that include specific spatial structure (catch statistical models such as CASAL, Stock Synthesis, Multifan-CL; and Age structure models like VPA2BOX) and others that attempt direct incorporation of the habitat environmental conditions (e.g., STATHBS). However, the main limitation of these applications is usually the transfer of fish between areas within the temporal stratification, although tagging experiments can provide information to infer movement rates.

Alternatively, habitat compression issues can be addressed directly in the standardization of catch rates. In principle, catch should be stratified spatially for similar vertical habitat structure, with depth of capture used as a proxy for different compression

habitats. For example, depth can be inferred in some situations from the gear configuration (e.g., the number of hooks between floats or the theoretical catenary shape of longline gear). However, experiments with electronic depth recorders on longline gear have shown that actual depth of the fishing gear is highly variable and dependent on oceanographic conditions, longline interactions with shipping or very large fish, etc. (Rice *et al.*, 2007). Other proxies for different habitats could be inferred from mean DO maps (Fig. 6), depth of thermocline as a function of time and area, or even temperature at depth profiles (Prince and Goodyear, 2006). The same stratification criteria could then be used for the definition of the spatial explanatory variable (e.g., area) in the CPUE standardization. The standardization model should also evaluate possible changes of the catchability factor as a function of time. This can be done by testing for significant interactions between year/area variables.

The above approach is clearly applicable to pelagic longline gear fisheries. However, because the size of the Atlantic habitat compression covers such a large area ($13 \times 10^6 \text{ km}^2$, Fig. 7) this phenomenon also greatly affects other gears. Not surprisingly, surface-oriented gears such as bait-boat and purse seines operate almost exclusively in compressed habitat areas (Fig. 7), where the stocks are more available to these types of gears (Prince and Goodyear, 2006). Developing indices for these gears should be restricted to specific habitat areas, using similar criteria for defining these areas, as described above. Attempting ocean-scale standardized indices of abundance, as described here, is likely to require additional research for practical application in the assessment process.

Climate change, global warming, oceanic acidification, and oxygen minimum zones

The impacts of the ETP and ETA OMZs on the management of tropical pelagic fishes should not be understated. This is particularly relevant considering the escalated pace of global warming and concurrent rise in ocean temperatures that would increase the size, hypoxic severity, and shoaling of these OMZs in the future (Rosa and Seibel, 2008; Stramma *et al.*, 2008, 2009). The synergistic effects of global warming and ocean acidification, relative to expansion of the OMZs, on high oxygen-demand tropical pelagic fishes and their preferred prey will predictably further reduce suitable habitat (Rosa and Seibel, 2008; Stramma *et al.*, 2008), while increasing vulnerability to higher levels of exploitation by surface fishing

gears (Prince and Goodyear, 2006). It remains to be seen whether the likely expansion of OMZs with global warming increases exploitation rates or rather dilutes the stocks sufficiently so that exploitation is little affected or declines. Therefore, the population status of tropical pelagic fishes in these areas should be monitored vigilantly to insure these stocks are not further diminished. In this regard, incorporating compression impacts into the stock assessment process seems essential, given the extensive geographical coverage of these oceanographic features in the tropical Atlantic and the escalated rate of global warming that will likely exacerbate future compression impacts.

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