Hypoxia-based habitat compression of tropical pelagic fishes

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ABSTRACT

Large areas of cold hypoxic water occur as distinct strata in the eastern tropical Pacific (ETP) and Atlantic oceans as a result of high productivity initiated by intense nutrient upwelling. We show that this stratum restricts the depth distribution of tropical pelagic marlins, sailfish, and tunas by compressing the acceptable physical habitat into a narrow surface layer. This layer extends downward to a variable boundary defined by a shallow thermocline, often at 25 m, above a barrier of cold hypoxic water. The depth distributions of marlin and sailfish monitored with electronic tags and average dissolved oxygen (DO) and temperature profiles show that this cold hypoxic environment constitutes a lower habitat boundary in the ETP, but not in the western North Atlantic (WNA), where DO is not limiting. Eastern Pacific and eastern Atlantic sailfish are larger than those in WNA, where the hypoxic zone is much deeper or absent. Larger sizes may reflect enhanced foraging opportunities afforded by the closer proximity of predator and prey in compressed habitat, as well as by the higher productivity. The shallow band of acceptable habitat restricts these fishes to a very narrow surface layer and makes them more vulnerable to over-exploitation by surface gears. Predictably, the long-term landings of tropical pelagic tunas from areas of habitat compression have been far greater than in surrounding areas. Many tropical pelagic species in the Atlantic Ocean are currently either fully exploited or overfished and their future status could be quite sensitive to increased fishing pressures, particularly in areas of habitat compression.

Key words: dissolved oxygen, habitat compression, hypoxia, overexploitation, tropical pelagic fishes, upwelling

INTRODUCTION

The depth distribution of suitable habitat is important to the ecology of pelagic fishes. Management of pelagic fisheries depends on adequate population estimates, often with methods that make assumptions about fish distributions (Brill and Lutcavage, 2001). Populations of Atlantic blue and white marlin (*Makaira nigricans* and *Tetrapturus albidus*, respectively) are considered overfished, while Atlantic sailfish (*Istiophorus platypterus*) are at least fully exploited or possibly overfished (ICCAT, 2004). However, recent stock assessments have been contested on the basis that alternate treatment of the depth distributions would possibly lead to a different conclusion (ICCAT, 2004). Very little data exist to characterize how most pelagic species actually utilize water depths (Block *et al.*, 1998; Brill and Lutcavage, 2001; Sibert and Nielsen, 2001) or how oceanographic features affect their distribution (Brill *et al.*, 1999; Brill and Lutcavage, 2001; Holland *et al.*, 2001). Here, we study vertical habitat use of istiophorid billfishes using electronic tags to evaluate possible avoidance of areas of naturally occurring hypoxia in the eastern tropical Pacific (ETP) Ocean and contrast this with data from the same species/ genera off the western North Atlantic (WNA) where dissolved oxygen (DO) is not limiting. We examine the consequences and possible causes of habitat compression relative to the ecology of these species and the fisheries that exploit them.

MATERIALS AND METHODS

Electronic tag deployments

Recent development of electronic tagging technologies (Block *et al.*, 1998), including pop-up satellite archival tags (PSAT), is revealing pelagic fish behavior that previously was not possible to observe (Sibert and Nielson, 2001). Compared to previous technology (i.e. acoustical telemetry), these tags provide an opportunity to extend monitoring durations (from hours and days to weeks and months) and provide a fishery independent means of data retrieval. The tags are attached externally to the fish where they log temperature, depth (pressure), and light data. The tags

detach after a user-defined interval and transmit summaries of the data through the ARGOS satellite system to a land station and then ultimately to the user via the Internet.

Deployment of PSAT tags on marlin and sailfish was conducted from recreational fishing vessels in both Pacific and Atlantic basins using standard trolling gear with natural bait or high-speed lures. All tag deployment activities were conducted within 50 miles of the coastline off south Florida, the Bahamas, Turks and Caicos Islands, and US Virgin Islands in the Atlantic and off Panama, Costa Rica, and Guatemala on the Pacific side of Central America. Wildlife Computers Inc.[1] (Redmond, WA, USA) PAT 3 model tags were the primary tags used, although a few PAT 2 model tags were used in 2000 and 2002. This tag allows the user to program pop-up date, sampling interval, criteria for premature release, bin demarcations for sampling temperature and pressure (depth), as well as transmission and memory priorities. These tags were programmed to sample depth (pressure), temperature and light once every 30 s or min, and the depth and temperature records were compiled into histograms at 6-hour intervals for most deployments. A few of the early deployments summarized histograms at 3-hour intervals.

The temperature bins were programmed for temperatures ≤12°C, each successive 2°C interval ending with 32°C, and >32°C. The depth bins included depths ≤−1, and successive intervals of 25–250 m, and depths >250 m. Samples were generally taken every 30 s and compiled into records reported for intervals of 6 h. A few tags were programmed to sample every minute. We compiled cumulative frequency distributions of time at depths and temperatures experienced by each fish and compared the results for each species/ genera between ocean basins. We also calculated the aggregate mean proportion of monitoring time and the mean proportion of records with one or more dives (to the maximum depth recorded in a record) within ≤50, >50, >100, and >200 m depth strata and compared results among species/genera/area treatments.

The thirty-two tags used in this study were programmed for deployment durations ranging from 7 to 90 days. A pressure-activated mechanical detachment device was also used which severs the 400-pound test monofilament tether at a depth of about 1500 m – well before the rated 2000-m crush depth of the tag. This feature helps prevent data loss in the event of fish

mortality. Release locations were obtained from global positioning systems onboard the tagging vessels and pop-up locations were obtained directly from the ARGOS transmissions of each tag. The data collected included the minimum and maximum temperature and depth, and amount of time spent in each of 12 specified depth and temperature bins for each sampled interval.

All PSAT tags were rigged in a manner similar to those described by Graves et al. (2002). Billfish handling and tagging procedures and associated devices reviewed by Prince et al. (2002) were also used. The target area for tag placement was about 4–5 cm ventral to the dorsal midline, adjacent to the first several dorsal spines (Fig. 1). An effort was made to insert the anchor through the dorsal midline, pterygiophores, and connective tissue to a depth just short of exiting the opposite side of the fish. In addition, a conventional streamer tag (series PS) was placed in the fish well posterior of the PSAT tag using standard procedures (Prince et al., 2002). Two devices were used during tagging which tend to reduce stress in captured fish and aid in proper tag placement. The first was a 'snooter' (a wire snare housed in a 1.5 m PVC tube, Fig. 1), which secures to the upper bill and allows the tagger to maintain control of the fish with its head beneath the water during the tagging procedure (Prince et al., 2002). The second was a small hook 'gaff' (a long shaft 9/0 hook with point and barb removed, Fig. 1) to manipulate the position of the fish relative to the tagging vessel. Captured fish were resuscitated from 3 to 15 min, depending on their apparent state of exhaustion, by moving the vessel ahead at two to three knots while maintaining control of the fish with the snooter.

Figure 1. A snooter (PVC pipe) and small hook gaff (wooden pole) are being used in tandem to control this Atlantic sailfish to ensure safe and precise placement of a PSAT tag.
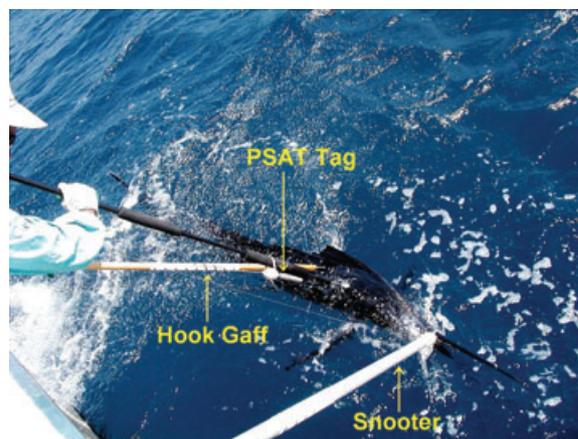
Figure 2. General study areas, with Pacific basin shown in blue (a) and Atlantic basin shown in red (b). Areas in both basins encompass horizontal displacements where electronic tags deployed on billfish transmitted to the ARGOS satellite system. Tag release locations within each study area are shown as stars (white).
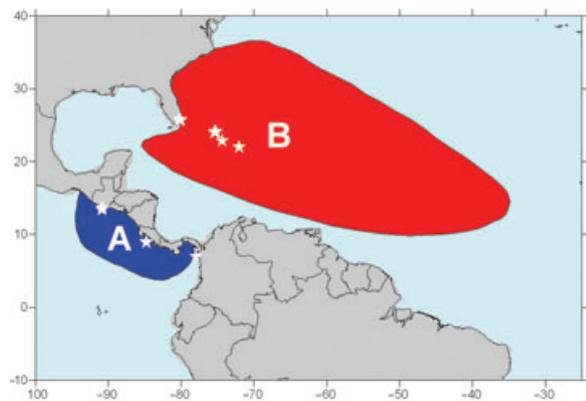
Data presentation and analysis

The boundaries of our PSAT study areas in the ETP and WNA were defined by the displacement vectors (point of release and point of first pop up of PSAT) of all billfish tagged in each area (Fig. 2). Virtually all release activities (shown as stars in Fig. 2) were accomplished within 50 nm of the shoreline of adjacent countries. A line connecting the end points represented by the pop-up location for each tag was drawn to form a circumference encircling displacement movements, and this served as the approximate boundary of study for each ocean basin (Fig. 2).

We analyzed the cumulative frequency of depth and temperature from PSAT data for marlin and sailfish using the general linear model (GLM) analyses with the univariate procedures of SPSS software. In the evaluation of the study areas, basin was included as a fixed variable, depth as a random variable, and the cumulative frequency of the percentage of time spent in each successively deeper depth was the dependent variable. In the analysis of temperature, basin was a fixed variable, temperature was a random variable, and the cumulative frequency of the percentage of time spent in each successively warmer bin was the dependent variable. We constructed the aggregate mean proportion of monitoring time and the aggregate mean proportion of records with one or more dives (to the maximum depth recorded in a record) within ≤50, >50, >100, and >200 m depth strata among species/area treatments. Arcsine transformations were made of the proportions of mean monitoring time and mean number of records with one or more dives among the four depth strata, and GLM procedures were then applied to test for differences in vertical habitat use among basins, species/genera, and depth strata. We also compiled average maximum depth from the composite ARGOS PSAT transmissions for each species/genera treatment for each study area. Our measure of dispersion about the means was one standard error.

We estimate oceanographic features likely encountered by our test animals by constructing distributions of temperature, DO, salinity, and chlorophyll at depth in the rectangles given by the co-ordinates of the tagging and pop-off locations for each month at large for each tagged fish pooled by study area. These compilations employed the objectively analyzed monthly means for each variable (by 1° of latitude and longitude) from the 1998 and 2001 World Ocean Atlas (WOA) (Conkright *et al.*, 1998; http://www.nodc.noaa.gov/OC5/). Dispersion about the mean temperature, DO, and salinity data are ±1 SD. The central tendency for chlorophyll is characterized by the median and dispersion by the 10th and 90th percentiles of the distributions. The annual distributions of mean depths of the mixed layer, depths at 3.5 mL L^{-1} DO, and DO concentration at 100-m depth are interpolated from the 1998 and 2001 combined WOA objectively analyzed monthly means by 1° of latitude and longitude using Surfer Version 8.3 (Golden Software). A separate analysis of the depths of the mixed layer is based on 1950–2002 monthly data by 2° latitude and 5° longitude from the Scripps Institution of Oceanography (SIO) (http://www.jedac.ucsd.edu/).

These features are contrasted with tropical tuna landings and the size composition of landed sailfish in different geographical areas. The catch distributions of skipjack and yellowfin tunas (*Katsuwonus pelamis* and *Thunnus albacares*, respectively) from the ETP and Tropical Atlantic are interpolated from 1950 to 2002, 5° latitude–longitude catch estimates obtained from the Food and Agriculture Organization of the United Nations (FAO; http://www.fao.org/fi/atlas/tunabill/english/downset.htm/) normalized to the maximum average catch in any 5° cell. Lengths of landed sailfish were obtained from the International Commission for Conservation of Atlantic Tunas (ICCAT) and the Inter-American Tropical Tuna Commission (IAT-TC). Where required, lengths of sailfish landings are converted from measured units to lower jaw fork length (LJFL) using the relationships in Prager *et al.* (1995).

RESULTS

Vertical habitat use of billfishes

From 2000 through 2003, we monitored 19 billfish (5 sailfish and 14 blue marlin) an aggregate of 801 days in the WNA, and 13 billfish (nine sailfish, three blue marlin and one black marlin, *Makaira indica*) an aggregate of 429 days in the ETP (Table 1). The general locations encompassing horizontal displacements (point of release and point of first pop-up location) in each ocean depict the general areas of study (Fig. 2). Taken together, these comparisons (cumulative frequency of depth and temperature and proportion of time at depth and at least one dive below the top of the stratum during a 6-hour period) provide a comprehensive view of vertical habitat use of the species/genera in the study areas in both ocean basins.

Cumulative depth frequencies indicated that both Atlantic marlin and sailfish tended to spend more time deeper in the water column than did their Pacific counterparts (Fig. 3a and b). Cumulative temperature frequencies were similar for Pacific and Atlantic marlin (Fig. 3c, $P = 0.78$); however, Pacific sailfish were observed more frequently in higher temperatures compared to Atlantic sailfish (Fig. 3d, $P < 0.01$), even though lower temperatures were available deeper in the Pacific water mass. Pacific sailfish also occasionally dove to depths with temperatures lower than Atlantic sailfish (Fig. 3b and d). These observations indicate our Atlantic and Pacific sailfish occupied different thermal niches and that environmental temperatures alone are not sufficient to quantify habitat.

In general, time at depth analyses indicated billfishes monitored in this study spent most of their time (i.e. > 70%) in the upper 50 m of the water column in both oceans (Fig. 4a). However, time at depth distributions of marlin and sailfish in the ≤50 m depth stratum in the Pacific were significantly shallower than their counterparts monitored in the Atlantic (Fig. 4a, $P < 0.01$ for both species/genera). This difference is evident in the binned proportions of time at depth that show our Pacific billfish spent significantly ($P ≤ 0.01$) more time (>90%) within the shallowest stratum (≤50 m) than did our Atlantic billfish (70–75%, Fig. 4a). The proportion of dive records in this stratum (≤50 m) for each species/genera was the same in both oceans – i.e. 100% of the dive records had at least one dive in this stratum (Fig. 4b). However, there were highly significant differences ($P < 0.01$) in time spent at depth, as well as the occurrence of dives below the >50 and >100 m depth strata for Atlantic billfishes compared to those monitored in the eastern equatorial Pacific. For example,

Atlantic billfish spent 25–35% of their time at the >50 m stratum, while Pacific billfish spent only 1–5% of their time in this stratum (Fig. 4a). In terms of the proportions of dive records, 80–85% of Atlantic billfish dove below 50 m at least once during each 6-hour period, while only 35–47% of Pacific billfish dove this deep (Fig. 4b). Progressively smaller numbers of dives were evident for the >100 and >200 m depth strata, but the relative difference between study areas increased with increasing depth. Although the deepest monitored depth stratum (>200 m) were infrequently utilized, Atlantic billfish made 10–100 orders of magnitude greater use of this deeper stratum than their Pacific con-specifics. This pattern is strongly reinforced by the deepest dives observed during successive 6-hour intervals while our tagged animals were at large (Fig. 5). Marlins were restricted to much shallower water in our Pacific study area compared to the Atlantic, and this behavior was persistent over the durations monitored (Fig. 5a). The pattern for sailfish was similar (Fig. 5b). The maximum depths and minimum temperatures recorded for each species/genera/area are also consistent with these trends, as follows: Atlantic sailfish max. depth = 284 m (15.8°C) verses Pacific sailfish max. depth = 144 m (15.2°C), and Atlantic blue marlin max. depth = 804 m (9.8°C), verses Pacific *Makaira spp.* max. depth = 108 m (18.3°C).

Sailfish landings in the study areas

Sailfish are reported to attain a greater size in the eastern Atlantic and Pacific than in the western Atlantic (Beardsley, 1980; ICCAT, 1994). We confirmed these findings with analyses of sizes of sailfish measured from surface gears in the Atlantic (ICCAT) and eastern Pacific (IATTC). The eastern Atlantic and Pacific exhibited remarkably similar average mean lengths of 183.9 cm LJFL in each basin and both were significantly larger than the 163.9 cm LJFL mean of samples from the western Atlantic ($P < 0.01$). In addition, the average size of sailfish landings in the eastern Pacific gradually showed a significant ($P < 0.01$) declining trend in LJFL as one moves westward from the Central American coastline (Table 2). Ultimately, in the most westerly longitude of 135° (on the westerly edge of the hypoxic plume shown Fig. 7b and c), the average size was about 164 cm LJFL, closely approximating the average size of 163.9 cm LJFL for WNA sailfish. Based on the most recent assessments, eastern Atlantic sailfish may be overfished while western Atlantic sailfish are fully exploited (ICCAT, 2004). Consequently, it seems unlikely that the differences in average size between
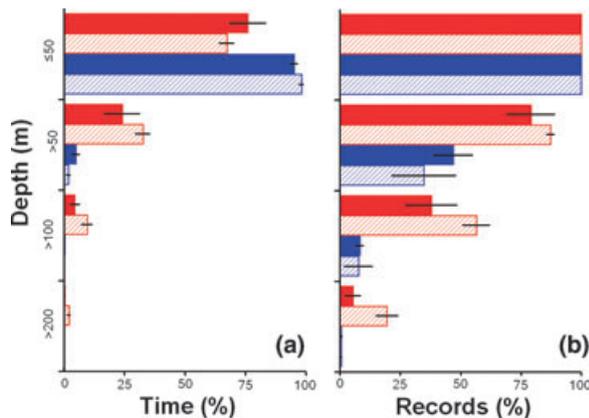
Table 1. Summary of pop-up satellite archival tag information for 32 Istiophorid billfish released from recreational gear in the western North Atlantic (WNA) and Eastern Tropical Pacific (ETP) basins, 2000–04. Species included sailfish (SAI), blue marlin (BUM), and black marlin (BLM). Tag number, date tagged, days monitored (DAL), displacement [distance in nautical miles (nm) between location of release and location of first transmission], ocean basin of release, and latitude and longitude for location of release and first transmission are also included.

	Tag number (ptt)	Species	Date tagged	DAL	Displacement (nm)	Ocean basin of release	Location of release	Location of first transmission
1	19572	SAI	08.12.00	31	153	ETP Guatemala	13.41.33N–90.85.17W	13.77.00N–99.46.00W
2	24397	SAI	09.08.02	28	34	ETP Panama	07.00.00N–78.00.00W	03.91.00N–63.40.00W
3	23077	SAI	03.10.03	30	90	ETP Costa Rica	09.79.70N–84.46.50W	07.92.00N–85.83.00W
4	23022	SAI	03.10.03	21	132	ETP Costa Rica	08.96.66N–84.78.00W	07.20.00N–85.59.00W
5	22870	SAI	03.10.03	40	447	ETP Costa Rica	08.96.66N–84.78.33W	08.82.90N–92.29.50W
6	22873	SAI	03.11.03	59	475	ETP Costa Rica	08.88.33N–84.78.33W	09.57.80N–92.78.30W
7	23002	SAI	03.11.03	29	161	ETP Costa Rica	08.96.66N–84.78.33W	07.57.30N–82.45.60W
8	25379	SAI	03.11.03	29	277	ETP Costa Rica	08.96.67N–84.76.67W	07.39.30N–89.15.00W
9	23442	SAI	03.12.03	29	176	ETP Costa Rica	08.95.00N–84.76.60W	06.53.30N–86.44.90W
10	19574	BUM	08.08.00	36	738	ETP Guatemala	13.89.50N–90.84.00W	08.66.00N–83.58.00W
11	23769	BLM	09.08.02	28	33	ETP Panama	07.00.00N–78.00.00W	07.45.50N–83.72.40W
12	1903	BUM	11.17.03	46	252	ETP Guatemala	13.63.44N–90.86.83W	11.01.20N–94.17.30W
13	19573	BUM	08.10.00	33	217	ETP Guatemala	13.39.39N–90.82.83W	14.34.00N–94.43.00W
14	39334	SAI	04.03.03	8	89	WNA Florida	25.74.47N–80.28.53W	26.72.60N–78.96.10W
15	39335	SAI	03.03.03	8	118	WNA Florida	25.83.33N–80.08.33W	27.80.20N–79.94.50W
16	33176	SAI	04.09.03	8	68	WNA Florida	25.81.50N–80.11.14W	24.81.20N–80.74.60W
17	33177	SAI	04.09.03	13	350	WNA Florida	25.69.20N–80.08.50W	31.52.60N–79.61.50W
18	40606	SAI	04.30.03	62	356	WNA Florida	25.69.20N–80.17.00W	26.60.20N–73.66.80W
19	41516	BUM	06.11.03	57	212	WNA Bahamas	24.04.80N–75.43.16W	27.24.50N–73.77.50W
20	41518	BUM	06.05.03	63	448	WNA Bahamas	24.05.00N–75.33.33W	31.19.90N–77.60.09W
21	41520	BUM	06.05.03	63	823	WNA Bahamas	24.10.00N–75.25.00W	36.86.00N–69.21.00W
22	41521	BUM	06.07.03	61	172	WNA Bahamas	24.10.00N–75.25.00W	22.25.00N–72.77.00W
23	41522	BUM	06.09.03	10	85	WNA Bahamas	24.08.30N–75.25.00W	25.08.10N–74.13.70W
24	41524	BUM	06.04.03	82	318	WNA Bahamas	24.10.00N–75.28.33W	19.07.20N–73.54.63W
25	41525	BUM	06.07.03	41	348	WNA Bahamas	24.11.67N–75.26.67W	29.90.70N–75.93.20W
26	41526	BUM	06.07.03	84	696	WNA Bahamas	24.11.70N–75.30.00W	35.70.30N–73.82.08W
27	41528	BUM	06.10.03	69	254	WNA Bahamas	24.11.20N–75.28.46W	28.26.40N–74.27.80W
28	41530	BUM	06.26.03	7	99	WNA Bahamas	22.85.30N–74.40.62W	24.49.60N–74.26.60W
29	41531	BUM	06.19.03	91	2157	WNA Turks and CA	21.99.97N–72.06.18W	14.25.30N–35.21.40W
30	41534	BUM	06.17.03	46	552	WNA Turks and CA	22.00.20N–72.06.86W	19.13.40N–62.77.55W
31	41538	BUM	06.16.03	47	1134	WNA Turks and CA	21.98.60N–72.03.48W	14.28.90N–54.03.60W
32	41539	BUM	06.18.03	74	92	WNA Turks and CA	21.98.70N–72.05.97W	20.62.40N–71.31.00W
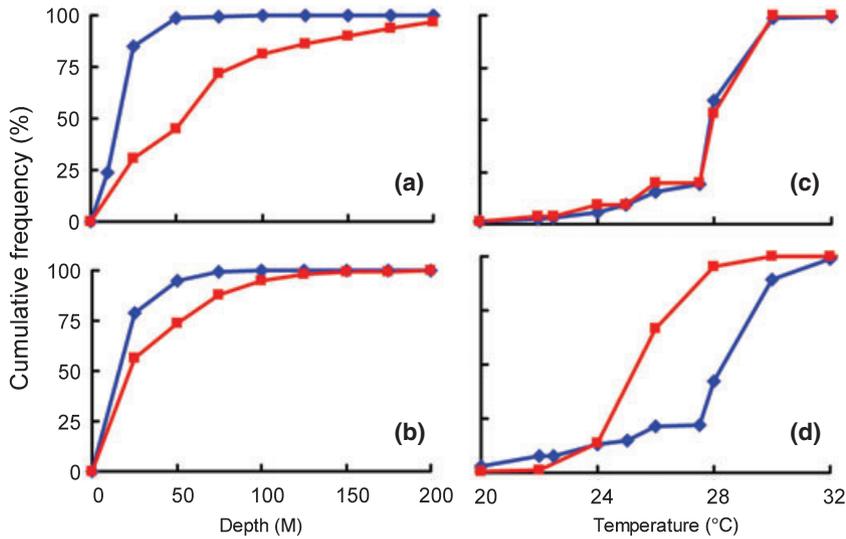
Figure 3. Cumulative frequency at depth for marlin (a) and sailfish (b) in Atlantic (red) and Pacific (blue) study areas and cumulative frequency at temperature for marlin (c) and sailfish (d) in the Atlantic (red) and Pacific (blue) study areas.

Figure 4. Proportion of time at depth (a) and proportion of records with dives to depth (b) for four depth strata (≤50, > 50, >100, and > 200 m) in Atlantic (red) and Pacific (blue) basin study areas for sailfish (solid color) and marlins (hatched bars). Horizontal error bars for proportion of time at depth and proportion of records with dives at depth are ±1 SE.

Figure 5. Average maximum depth (m) of marlin in the Pacific (blue solid line) and Atlantic (red solid line) study areas (a); and average maximum depth of sailfish in the Pacific (blue solid line) and Atlantic (red solid line) study areas (b). Errors for average maximum depth (shaded areas) of mean values are ±1 SE.

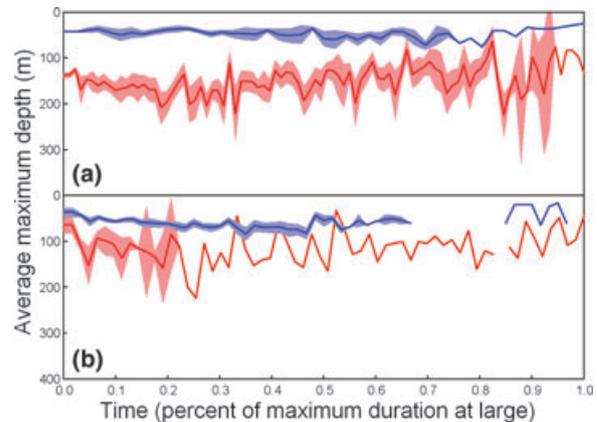the Eastern and Western Atlantic are a consequence of differential fishing mortality.

DISCUSSION

We believe the markedly different patterns of vertical habitat use between the Pacific and Atlantic ocean basins are a result of the different oceanographic features that typify the two study areas. The ETP study area is characterized by intense nutrient upwelling with a cool, very shallow thermocline (about 25 m), high surface chlorophyll (down to about 50 m), and DO profiles exhibiting hypoxic conditions

(≤2 mL L^{-1}) below the shallow thermocline (Fig. 6a–d). Conversely, the WNA study area is part of the subtropical gyre, with a large, warm surface layer, a deep thermocline (about 75 m), lower surface chlorophyll, and DO profiles that exceed 4.0 mL L^{-1} for depths ≤300 m (Fig. 6a–d). Of the four oceanographic features depicted in Fig. 6 (temperature, DO, salinity, and chlorophyll), the greatest disparity between ocean basins was clearly the differences in DO profiles. The higher surface chlorophyll levels in the ETP are due to the intense nutrient upwelling that defines this area. Although surface temperature in both basins was similar, the ETP was universally cooler at virtually all depths than the WNA. Salinity of the ETP was always

Table 2. Mean lengths (Lower Jaw Fork Length, LJFL cm), standard errors, and lower and upper 95% confidence intervals for sailfish landings from the eastern tropical Pacific purse seine fishery.

Longitude	Mean	SE	95% Confidence interval	
			Upper bound	Lower bound
75	200.510	0.797	198.948	202.072
80	201.713	0.705	200.331	203.095
85	200.792	0.564	199.686	201.898
90	197.563	0.734	196.125	199.002
95	194.938	0.685	193.596	196.280
100	180.227	1.072	178.126	182.328
105	186.143	0.636	184.896	187.389
110	177.963	1.967	174.106	181.819
115	169.867	3.687	162.640	177.094
120	166.950	2.695	161.667	172.233
125	166.033	5.552	155.159	176.916
135	164.487	10.752	143.409	185.565

Data were obtained from the IATTC. Landings are presented by longitude, starting near the Central American coastline at 75° W and moving westward to 135° W.

lower at each depth strata than the NWA but differences in salinity were small (ranging from about 33 to 36.8) and appear to be inconsequential.

Average depth of the surface mixed layer that marks the top of the thermocline predicts several biologically important oceanographic features. The surface mixed layer is much shallower in the Pacific study area than in the Atlantic study area (Fig. 7a). Our results on vertical habitat use of billfishes may be partly explained by the fact that the depth at temperature is predictably shallower in the Pacific than in the Atlantic. However, Pacific sailfish tended to spend more of their time in shallower depths and higher temperatures than those in the Atlantic, but occasionally dove into lower temperatures than did our Atlantic sailfish. Also, although the cumulative frequencies of time at temperature for our Atlantic and Pacific blue marlins were similar, Atlantic blue marlin made dives into much colder water than did their Pacific counterparts. These observations suggest some factor(s) other than temperature alone is contributing to the differences between the two basins.

We hypothesize that, in addition to temperature, variations in DO concentrations play an important role in limiting the depth of the acceptable habitat for billfish and other tropical pelagic fishes. These fish rely on forward movement to irrigate their gills (obligate ram ventilation) in order to sustain respiratory function and support their unusually high metabolic rates (Roberts, 1978; Pauly, 1981; Brill, 1996). Studies of

the oxygen requirements of some small (≤75 cm fork length) skipjack and yellowfin tuna indicate that lethal DO levels appear to range from 2.16 to 1.87 and 1.77 to 1.14 mL L^{-1} for the two species, respectively (Brill, 1994). However, DO levels ≤3.5 mL L^{-1} induce symptoms of stress, and we adopt this concentration as the hypoxic threshold for these species (Ingham *et al.*, 1977; Gooding *et al.*, 1981; Bushnell and Brill, 1991). The oxygen requirements of sailfish and marlins are poorly known, due, in part, to the difficulty in holding these species in captivity (Post *et al.*, 1997) and the lack of technology for long-term monitoring (Holland *et al.*, 2001). However, measurements of oxygen consumption of juvenile sailfish (Idrisi *et al.*, 2002) indicate that this species has the high oxygen consumption and associated metabolic rates typical of tropical tunas (Roberts, 1978; Brill, 1996). We believe the hypoxic threshold for tropical pelagic istiophorid billfishes is similar because these species share the metabolic characteristics of tropical tunas.

DO depletions have been observed to modify the extent of acceptable habitat for estuarine and coastal fishes (Eby and Crowder, 2002). Similarly, fishes around Gulf of Mexico reef and oil structures move upward in the water column to avoid seasonally hypoxic conditions in the deeper portions of their habitat, a behavior that also increased their density (Stanley and Wilson, 2004). Several authors have previously only speculated that DO levels in some areas of the equatorial Pacific and Atlantic reach values low enough to inhibit vertical movement of some tropical pelagic fishes (Green, 1967; Sund *et al.*, 1981; Brill *et al.*, 1999; Bakun *et al.*, 1999; Levin, 2003). However, extensive continuous empirical data on vertical habitat use of sailfish, marlin, and tropical tunas were not available in the past to test this hypothesis. In our study areas, DO at 100 m depths averages below 1.5 mL L^{-1} in the Pacific, compared to above 4 mL L^{-1} in the Atlantic (Fig. 7b). The pattern of annual average shallowest depths of the 3.5 mL L^{-1} DO isopleths (our hypothesized hypoxic threshold) for the eastern Atlantic and eastern Pacific (Fig. 7c) closely tracked the average depth of the surface mixed layer depicted in Fig. 7a and d. Both the surface mixed layer and depth at 3.5 mL L^{-1} DO isopleths are shallowest off our study area along the Pacific coast of Central America in the ETP and along the west coast of Africa in the eastern tropical Atlantic (ETA).

The relatively shallow depths of hypoxia and surface mixed layer in the ETA and ETP appear to be remarkably stable, if not a permanent feature (Diaz, 2001; Helly and Levin, 2004). In fact, Helly and Levin (2004) describe naturally occurring upwelling induced

Figure 6. Temperature (degree Celsius, a), dissolved oxygen (DO, mL L^{-1}, b), salinity (ppt, c) and chlorophyll (μg L^{-1}, d) profiles derived from 1998 and 2001 World Ocean Atlas data for the Atlantic (red) and Pacific (blue) study areas. Temperature, DO, and salinity data are means and horizontal error bars are ±1 SD. Chlorophyll data are the median and horizontal error bars are for the 10th and 90th percentiles of the distribution of values within included cells.
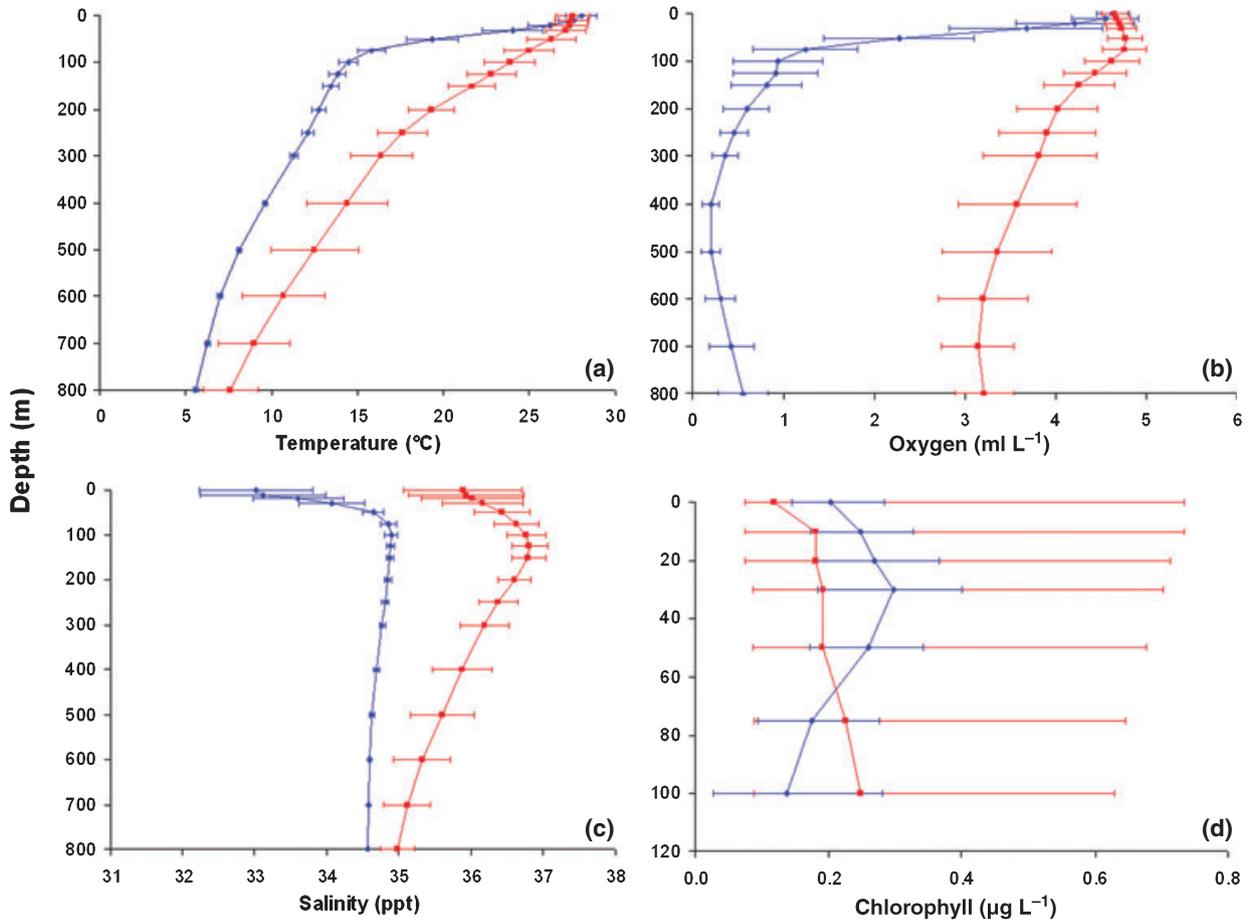
hypoxia as a permanent oceanographic feature in large areas of the ETP and ETA Oceans. This is primarily a function of the prevailing weather patterns and other oceanographic processes that define these areas. For example, the average depth of the surface mixed layer based on WOA data in 1998 and 2001 (Fig. 7a) is almost identical to the same plot for each year separately, and also to the means determined from SIO data (Fig. 7d) for an extended time series (1955–95). Consequently, we believe these DO profiles are reasonable approximations of the conditions that existed during our study, which was conducted in 2000, 2002, and 2003, primarily during spring, summer, and fall months. Although El Nino episodes can have strong

annual and inter-annual influence on the thermal regimes in the upper water layers and tend to depress the thermocline, these effects are most acute in near shore waters in the ETP (Bakun, 1996). Alternatively, La Nina episodes would have the opposite affect of influencing the thermocline shallower. However, the hypoxic environment below the thermocline remains, to a large extent, unaffected (Bakun, 1996). During the years when we deployed PSATs in the ETP (2000, 2002, 2003), no major El Nino episode occurred in ETP (IRI Website, http://iri.columbia.edu). Thus, the depth of the thermocline or the extent of hypoxia below the thermocline would not have been impacted significantly, particularly in offshore areas where the

Figure 7. Isopleths of average depth of the surface mixed layer from 1998 and 2001 WOA data (a), isopleths of DO concentrations at 100 m depth (b), isopleths of the average depths of the 3.5 mL L^{-1} DO (c), and isopleths of the average depth of the surface mixed layer from 1950 to 2002 SIO data (d). A dashed line indicates study areas shown in Fig. 1.
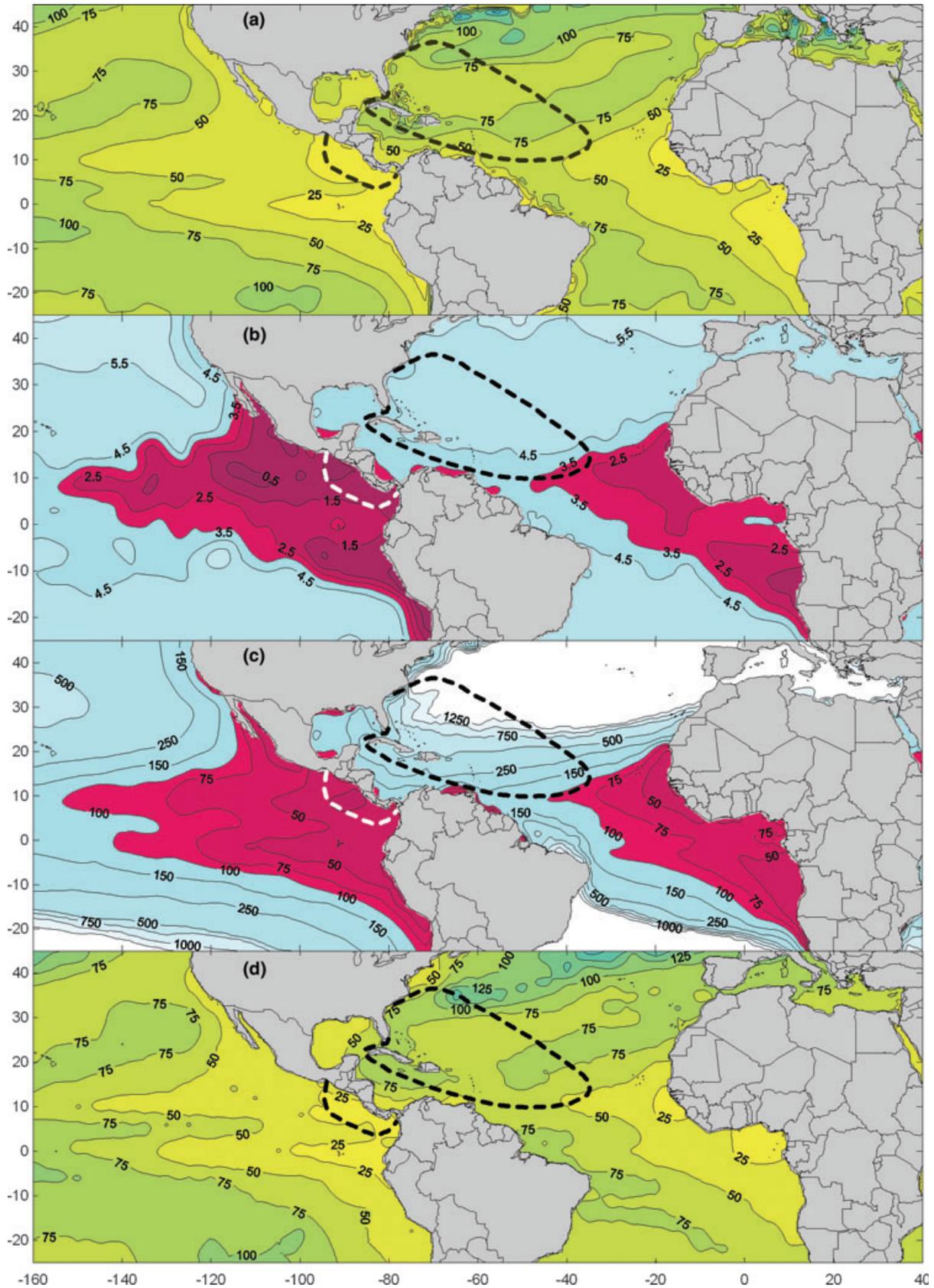
tagging took place. Moreover, hypoxic conditions existed at depths less than 50 m in the eastern Pacific, but not in the eastern Atlantic (Fig. 7b and c). Further, the DO concentrations of less than 1.5 mL L^{-1} at 100 m in the Pacific study area (Fig. 7b) are probably below lethal continuous-exposure levels for istiophorid billfishes.

DO conditions are consistent with the observed differences in the depths utilized by our billfish in the two study areas. DO levels of 1.5 mL L^{-1} occur between 50 and 75 m in our Pacific study area (Fig. 6b). This depth range corresponds to the deepest habitat use for both marlins and sailfish along the Pacific coast of Central America (Fig. 5a and b). Conversely, in the Atlantic study area DO at 400 m averaged about 3.5 mL L^{-1}, and remained above 3.0 down to 800 m (Fig. 6b). These levels would not be expected to prohibit habitat use by marlin or sailfish and are consistent with their observed depth utilization (Fig. 5a and b). As evidenced by an observed blue marlin dive (804 m, ≤9.8°C), where DO is not limiting, istiophorid billfishes, particularly blue marlin, can dive into deep, cold water for short periods. This diving behavior is no doubt facilitated by their brain heater (Block, 1986) that permits ocular and physical function at low temperatures (Block, 1986; Block and Finnerty, 1994; Fritsches et al., 2003,2005).

There are a number of oceanographic features that influence the occurrence, distribution, and magnitude of DO depletions that occur in the Eastern Atlantic and Eastern Pacific equatorial regions. The upwelling process in these areas brings nutrients to the surface waters where phytoplankton growth is enhanced (Wyrtki, 1965; Bakun et al., 1999). These areas are some of the most productive marine environments in the world (Cushing, 1969). Productivity driven by these nutrient-enriched environments is transferred up the food chain through primary and secondary producers, to provide the bulk of the food base for forage fishes (small scombrids, carangids, and clupeids) that ultimately sustain the tropical pelagic predators (Cushing, 1969; Brock, 1984). The high productivity results in a rain of biological material that sinks into the upwelling water mass. Concurrent changes in temperature, the depth of the thermocline, and size of the mixed layer that extends from the top of the thermocline to the surface are all consequences of the upwelling process (Cushing, 1969). The subsequent in situ decomposition of organic matter at depth, stagnant deep water layers, the advection process and absence of significant mixing in these areas all contribute to the development of hypoxic environments (Cushing, 1969; Levin, 2003) where low DO

Figure 8. Distribution of skipjack and yellowfin tuna catch estimates by surface gears in the Atlantic and eastern Pacific Oceans from FAO data, 1955–2000. Catches were normalized to the maximum average catch per 5° cell.
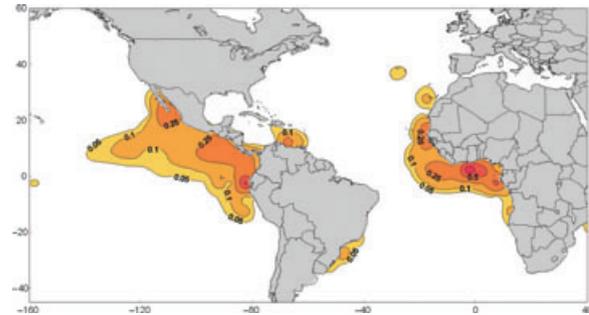
concentrations would be physiologically stressful to tropical pelagic fishes (i.e. marlins, sailfish, and tropical tunas).

Consequences of habitat compression

The extremely shallow depth of acceptable habitat in these areas restricts the productive environment to the near surface, which increases the vulnerability of pelagic predators to surface fishing gears. This premise is supported by purse seine experiments where tropical tuna consistently escaped by diving below the net bottom when the depth of the net was above the thermocline (Murphy and Niska, 1953). Conversely, in areas where the acceptable habitat is very shallow and fishing gear extends below the thermocline (Barkely et al., 1978), escapement by tunas diving under the bottom of purse seines is hindered considerably and results in more successful purse seine sets (Brock, 1959; Green, 1967). The availability of these species to other surface gears, such as hand lines and surface longlines, should also be enhanced. That this process enhances catch rates of tropical pelagic species is evident from the high yellowfin and skipjack tuna catches in the eastern Atlantic and eastern Pacific (Fig. 8). Both species are cosmopolitan in the tropical oceans, but their harvest is markedly elevated in the areas where acceptable habitat in the ETP and ETA is bounded by cold, hypoxic conditions below the shallow thermocline. Periodic reports of large catches of billfish from the tropical purse seine vessels fishing in eastern equatorial regions in both ocean basins (personal communication, A. Fonteneau, September 26, 2004 and [2]) are consistent with this view.

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[2]Sport Fishing Magazine (2003). Caught in the act: sailfish slaughter in Panama. Sept./Oct. Issue. pp. 14–15.

Besides increasing the vulnerability and exposure of tropical pelagic fishes to surface gears, habitat compression also facilitates closer physical proximity of predator and prey in the same habitat. Because the preferred prey of marlin and sailfish (primarily small scombrids, clupeids, and carangids, Beardsley *et al.*, 1975; Rivas, 1975; Brock, 1984) are ram ventilators with similar oxygen needs (Roberts, 1975, 1978; Brill, 1996), habitat compression would predictably constrain both predator and prey to near surface waters. The resulting enhanced foraging opportunity may explain the differences in mean size of sailfish in the ETP and ETA as compared to WNA. Large catches (Cushing, 1969) and large average size of landings (Beardsley, 1980) of pelagic fishes taken from eastern equatorial regions are normally attributed only to the high productivity from upwelling. However, habitat compression may also contribute to these trends.

The hypoxic environments have special significance for recreational catch and release fisheries and conservation-motivated releases of pelagic fishes taken on commercial gear in such areas. The accumulation of oxygen debt during the fish's capture makes it less able to survive exposure to hypoxic conditions upon release. If it is not sufficiently recovered to avoid sinking into hypoxic depths, sometimes less than 25 m below the surface, it is unlikely to survive. Released billfish and tropical tunas must sustain horizontal forward movement for respiratory function and to remain above the hypoxic environment. Without applying resuscitative techniques to ensure survival (Prince *et al.*, 2002), many fish stressed from the capture experience, but released alive in these areas, may succumb to the hostile environment below the thermocline.

Habitat quantification is also an important problem for estimating population trends from longline catch per unit effort (CPUE) time series for pelagic species. Results of recently introduced models that standardize CPUE time series based on habitat considerations (habitat standardizations) often differ substantially from those based on formal statistical procedures. In the case of Atlantic blue marlin, the application of the habitat standardization model of Hinton and Nakano (1996) estimated much smaller declines in stock abundance than estimated with traditional statistical methods (ICCAT, 2001). Such contradictory results promote uncertainty in the interpretation of stock assessment results (ICCAT, 2004). Simulation studies of the robustness of habitat standardization methods demonstrated that errors in the quantification of the habitat can lead to serious error in the resulting estimates of population trends

(Goodyear, 2003). The Hinton and Nakano (1996) method quantifies habitat solely on the basis of temperature relative to the temperature of the surface mixed layer. This temperature differential relative to the surface mixed layer (i.e. delta T of 8°C) was also mentioned by Brill *et al.* (1993) as a factor determining the maximum depth of istiophorids near Hawaii. Our results strongly suggest oxygen concentrations are also important determinants of blue marlin habitats. Omission of DO from the habitat quantification may seriously compromise the habitat standardizations of CPUE trends. Bigelow *et al.* (2002) recognized the importance of oxygen as a component of bigeye tuna (*Thunnus obesus*) habitat and included this feature in a CPUE habitat standardization model for the species in the Pacific. However, Ward and Myers (2006) demonstrated that the Bigelow *et al.* (2002) model did not accurately predict the depth distribution of bigeye tuna, and that statistical models provided superior results. These findings possibly reflect an inadequate quantification of the relative importance of temperature versus DO, or the omission of a critical habitat element. The habitat-standardization approach offers much promise, but its utility will remain uncertain until the relevant features of the habitat can be adequately quantified. For billfish this will require models that integrate temperature, depth and possibly other relevant habitat factors.

Potential causes of habitat compression

Where the depth of acceptable habitat is clearly limited by hypoxic conditions, temperature and DO concentrations are highly correlated because both decline with increasing depth (Fig. 6a and b). This feature obfuscates the importance each variable plays in defining acceptable habitat for tropical pelagic species. The high-performance physiology (Brill, 1996), which leads to a relatively high hypoxic threshold of tropical pelagic fishes, including istiophorids (about 3.5 mL L^{-1}, Brill, 1996; Idrisi *et al.*, 2002), makes these species dependent on an oxygen-rich environment, that in the ETP exists only near the surface. In addition, the DO concentrations between 75 and 100 m in the Pacific study area are likely below lethal continuous-exposure levels ($\leq$1.5 mL L^{-1}) for istiophorid billfishes. Randall (1970) observed that teleosts 'become more active in hypoxic conditions and attempt to leave the oxygen-depleted environment.' This behavior would foster compression of affected populations into the remaining suitable habitat. We suspect that where DO is below physiological requirements, it is a more important constraint on

habitat utilization than temperature (Randall, 1970; Diaz, 2001).

However, habitat is not defined by a single variable. Rather, it is defined by the complex of factors that promote species viability. In the ETP, where the habitat for tropical pelagics is limited to the very near surface by a cold hypoxic environment below a shallow thermocline, factors other than oxygen are also important to the environment. The intense nutrient upwelling in the surface mixed layer (as evidenced by the high chlorophyll levels, Fig. 6d) is the basis for one of the most productive marine environments in the world. Preferred prey organisms must also avoid the cold hypoxic zone and remain in the surface mixed layer to feed on primary and secondary producers, thereby restricting the depth distribution of the billfish forage and reducing the need for billfish to explore deeper into the water column. Temperature, oxygen, primary productivity, prey distribution, and undoubtedly a host of other factors interact to define the habitat of tropical pelagic species.

CONCLUSION

We have presented strong quantitative evidence that the depth of the acceptable habitat for billfish is shallower in our eastern Pacific study area than the WNA. We contend that this result is a consequence of the different oceanographic features of the two ocean basins, particularly the shallow thermocline and underlying hypoxia in the ETP that is not present in the WNA. There are convincing reasons to believe that our findings apply to the eastern Atlantic and to other tropical pelagic species as well. The same features of the environment that limit the acceptable habitat to a very narrow surface layer also make the fishes more vulnerable to exploitation, as evidenced by high catches of tropical pelagic tunas in these areas. Many of these species are currently either fully exploited or overfished and considering the concentration effects of habitat compression, we should be especially vigilant in monitoring the catch and effort in these areas to insure that the status of the resources are not diminished. Our results provide new insights into how oceanographic features influence the habitat of tropical pelagic fishes and the fisheries that exploit them.

ACKNOWLEDGEMENTS

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