 Manuscript received November 17, 2007; accepted March 6, 2007

# CONSEQUENCES OF OCEAN SCALE HYPOXIA CONSTRAINED HABITAT FOR TROPICAL PELAGIC FISHES

**Eric D. Prince[1] and C. Phillip Goodyear[2]**
*[1]National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149 USA, E-mail eric.prince@noaa.gov*
*[2]1214 North Lakeshore Drive, Niceville, Florida 32578 USA*

*ABSTRACT* Large areas of cold hypoxic water occur as distinct strata in the eastern tropical Pacific and Atlantic oceans as a result of high productivity initiated by intense nutrient upwelling. Recent studies show that this stratum restricts the depth distribution of tropical pelagic marlins, sailfish, and tunas in the eastern tropical Pacific 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 mean dissolved oxygen (DO) and temperature profiles show that this cold hypoxic environment constitutes a lower habitat boundary in the eastern tropical Pacific, but not in the western North Atlantic, where DO is not limiting. However, hypoxia-based habitat compression has not actually been demonstrated in the eastern tropical Atlantic Ocean, despite this region having similar oceanographic features to the eastern tropical Pacific. This paper explores the possibility that habitat compression of tropical pelagic fishes exists in the eastrn tropical Atlantic and examines possible consequences of this phenomenon. We used Atlantic-wide catches of yellowfin tuna (*Thunnus albacares*) as an example why habitat compression off west Africa could eventually affect the total Atlantic stock.

*RESUMEN* Extensas areas con aguas relativamente frias y bajo contenido de oxigeno (hypoxia) pueden ocurrir en el Pacifico y Atlantico Tropical oriental como resultado de alta productividad biologica en zona de upwelling. Estudios recientes demuestran que estos estratos restringen la distribucion vertical de species pelagicas tropicales como los marlines, pez vela y atunes en el Pacifico tropical oriental al comprimir el habitat de estas especies a una termoclina poco profunda, a menudo solo 25 m, sobre una barrera de agua fria y con bajo contentido de oxigeno. Las distribuciones vertical de marlines y pez vela monitoreadas con marcas eletronicas y perfiles de oxigeno disuelto (OD) y temperature muestran que este ambiente relativamente frio y bajo contenido de oxigeno constituye una barrera del habitat en el Pacifico tropical oriental, pero no el Atlantico Norte occidental donde el OD no es limitante. La compresion del habitat basada en la hypoxia no se pudo demostrar en el Atlantico tropical oriental, a pesar de que esta region tiene caracteristicas oceanograficas similares a las del Pacifico tropical oriental. Este documento explora la posibilidad de la existencia de habitats comprimidos para especies de peces tropicales y examina las posibles consecuencias de este fenomeno. Utilizamos colectas de albacore (*Thunnus albacores*) como ejemplo del efecto de la compresión del habitat en la parte oeste de Africa y su efecto en el stock del Atlantico.

Large areas of cold, oxygen-depleted (hypoxic) waters are permanent features of the eastern tropical Pacific and Atlantic oceans (Helly and Levin 2004), a result of intense nutrient upwelling (Cushing 1969, Diaz 2001). Here we use electronic tags (Siebert and Nielson 2001) to show that these cold, hypoxic strata compress the acceptable physical habitat of marlin and sailfish into a shallow surface layer, with important ecological and fisheries consequences.

Very little data exist to characterize the habitat depths of tropical pelagic billfishes and tunas, even though these features are critical for monitoring population abundance. We investigated habitat depth of marlin and sailfish using popup satellite archival tags (PSAT, Siebert and Nielson 2001). We monitored 19 billfish an aggregate of 801 d in western North Atlantic habitats where dissolved oxygen (DO) concentrations are not limiting, and 13 billfish an aggregate of 429 d in the eastern tropical Pacific, where hypoxic conditions are often as shallow as 25 m (Figure 1A). We stratified the amount of time spent by each fish, and its deepest dive during successive 6 hr periods into strata of $\leq 50$ m, $> 50$ m, $> 100$ and $> 200$ m. Pacific billfish remained within the shallowest strata, while Atlantic billfish were much more likely to venture deeper (Figure 1B, a & b). Our analyses showed markedly different vertical habitat use (highly significant $P < 0.001$) in the two studies areas.

The spatial extents of acceptable habitats for some estuarine and shallow demersal reef fishes are known to respond to variation in DO (Eby and Crowder 2001, Stanley and Wilson 2004). Our findings show this phenomenon also exists at a much larger scale for pelagic fishes in the tropical oceans. In our Pacific study area, DO levels (Fonteneau 1997, Prince and Goodyear 20061) of

[1]The contours of annual mean DO (ml/l) were interpolated from 1998 and 2001 World Ocean Atlas (http://www.nodc.noaa.gov/OC5/) objectively analyzed monthly means by 1º of latitude and longitude using Surfer V 8.3 (Golden Software). Methods for developing mean DO profiles and mean maximum depth of marlins and sailfish in our study areas are given in Prince and Goodyear (2006).

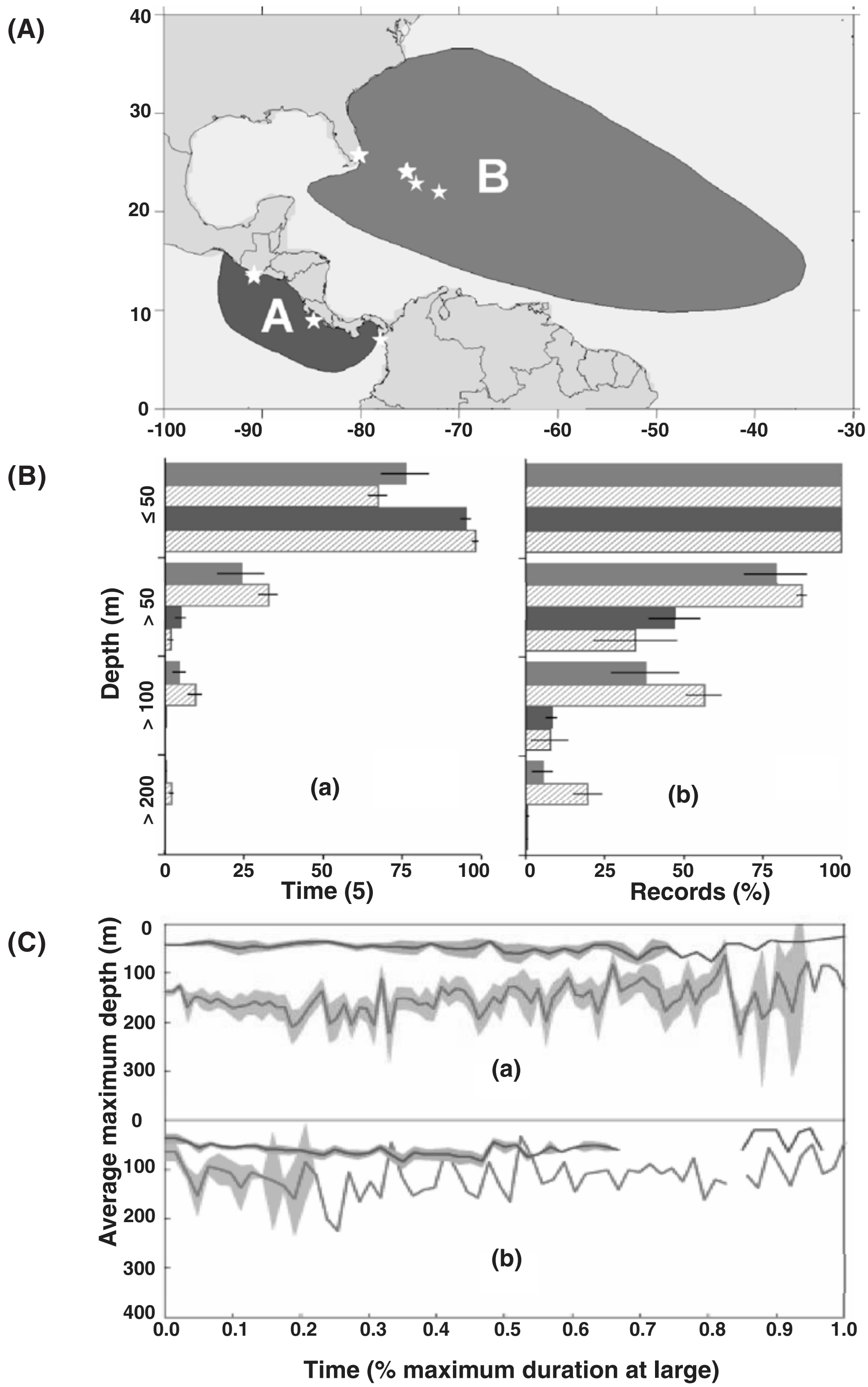


**Figure 1. (A) Pacific (A) and Atlantic (B) basin study areas as defined by the displacements of electronic tags deployed on billfish from point of release (stars) to where the tags transmitted data to the Argos satellite system. (B) Proportion of time at depth (a) and proportion of records with dives to depth (b). Atlantic and Pacific billfish are denoted by red and blue, respectively. Solid bars represent sailfish and crosshatched bars denote marlins. Error bars are one standard error. (C) Maximum observed depths of marlin (a) and sailfish (b) during successive 6-hr intervals after release (Prince and Goodyear 2006). Pacific observations are above the Atlantic observations, respectively, and shaded areas denote variability (± one $s_{\bar{x}}$). Solid lines represent the 6-hour average maximum depths visited by each species. Reprinted with permission from the Journal of Fisheries Oceanography 15(6):451–464, 2006.**

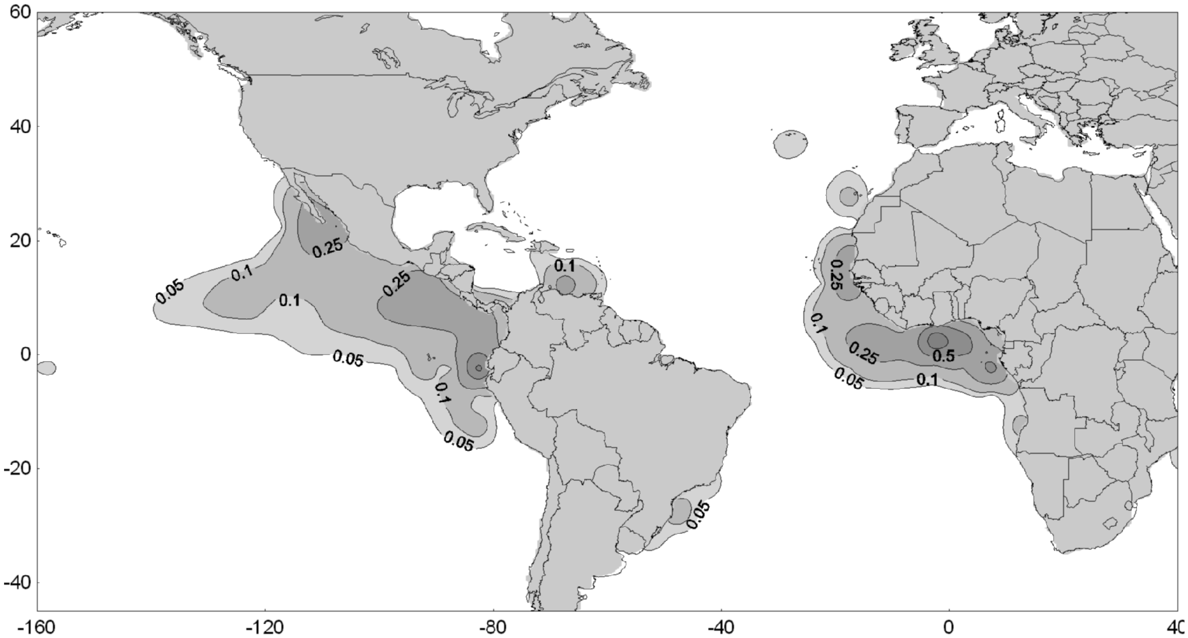


**Figure 2. Distribution of skipjack tuna and yellowfin tuna catch estimates in the Atlantic and eastern Pacific Oceans from FAO data, 1955–2000. Catches were normalized to the maximum average catch per 5$^{o}$ cell. Reprinted with permission from Fisheries Oceanography 15(6):451–464, 2006.**

1.5 ml/l occur at about 75 m and this depth appears to form the lower threshold of habitat use for our Pacific billfish (Figure 1C, a & b). Conversely, DO levels rarely fell below 3.5 ml/l (Fonteneau 1997, Prince and Goodyear 2006) and did not appear to constrain vertical habitat use of our Atlantic marlin or sailfish (Figure 1C). The extremely shallow depth of acceptable habitat in the Pacific study area arising from nutrient upwelling in the region also restricts this highly productive environment to the very near surface. We feel that this habitat compression facilitates closer physical proximity of predator and prey in the same habitat, which would provide enhanced foraging opportunities that may contribute to faster growth and larger mean sizes of apex predators (Beardsely 1980, Prince and Goodyear 2006).

We have discovered strong quantitative evidence that the depth of the acceptable habitat for billfish is shallower in our eastern Pacific study area than the western North Atlantic. We contend that this difference is a consequence of the cold hypoxic water underlying the shallow thermocline in the eastern Pacific, not present in the western North Atlantic. The same environmental features that limit acceptable habitat to a very shallow surface layer also make the fishes more vulnerable to exploitation, as evidenced by high catches of tropical pelagic skipjack and yellowfin tunas in these areas (Figure 2). Where the habitat is compressed into a shallow surface layer, fish are fully exposed to highly efficient surface gears such as purse seines, a combination that can threaten resource productivity and sustainability. This vulnerability is particularly important for bycatch species like blue marlin that have lower tolerances to fishing mortality than the target species, e.g., yellowfin tuna (Goodyear 2005).

Although the eastern Atlantic has many of the same oceanographic features of the eastern tropical Pacific (Fonteneau 1997, Prince and Goodyear 2006), Atlantic habitat compression of tropical pelagic fishes has yet to be documented with empirical data (Prince and Goodyear 2006). If hypoxia-based habitat compression does exist in the eastern Atlantic, the question becomes: Is this an issue of concern in the western north Atlantic? The International Commission for the Conservation of Atlantic Tunas (ICCAT) manages yellowfin tuna as a total Atlantic stock and this stock structure hypothesis is confirmed, in part, by conventional tagging results that demonstrate connectivity on both sides of the Atlantic (Figure 3). As many of these species are already fully exploited or overfished, increased vulnerability of yellowfin tuna in compressed habitat off West Africa could eventually affect the entire Atlantic stock.

## ACKNOWLEDGMENTS

The Billfish Foundation supported CPG's contribution to this work.

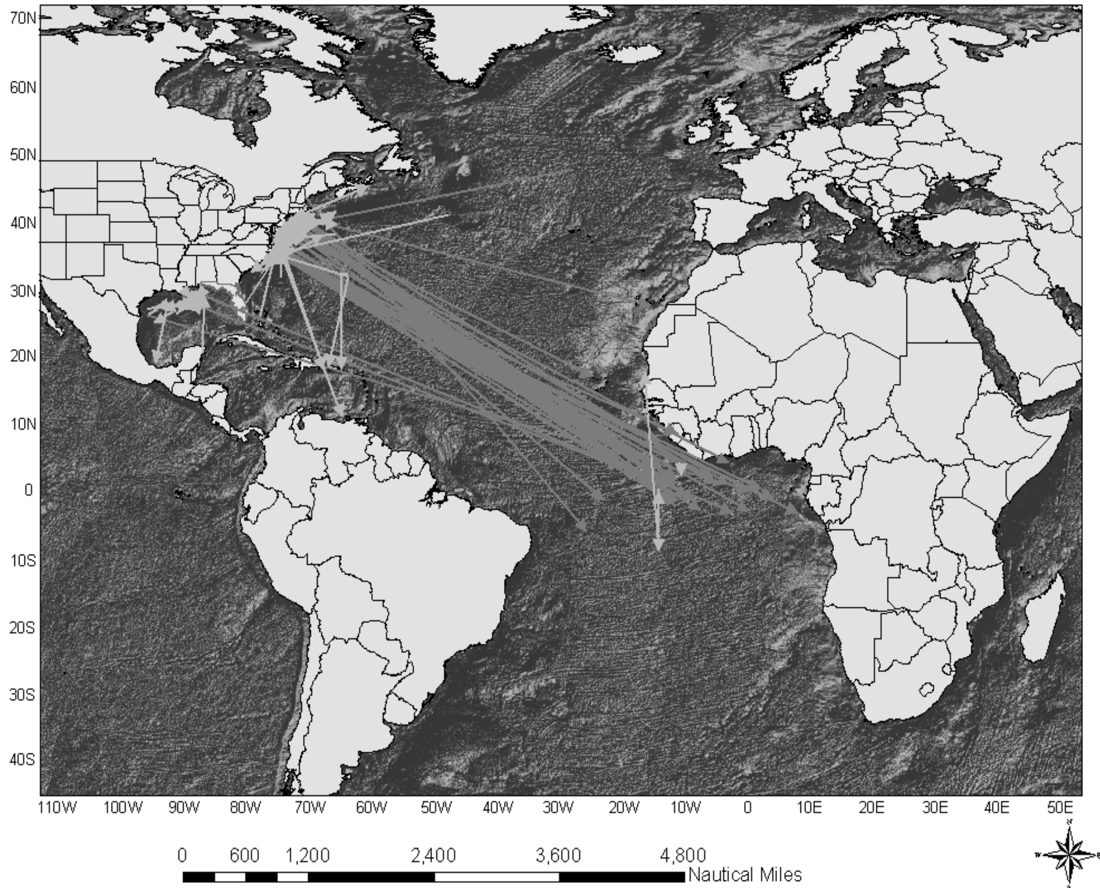


**Figure 3. Conventional tag recoveries for yellowfin from the Southeast Fisheries Science Center's Cooperative Tagging Center, Miami, FL., 1954–2005. Red displacements illustrate transatlantic movements and yellow displacements show western or eastern Atlantic movements. Arrows indicated direction of movement.**

## LITERATURE CITED

Beardsely, G.L. 1980. Size and possible origin of eastern Atlantic sailfish. Fishery Bulletin 78:805–808.

Cushing, D. 1969. Upwelling and fish production. FAO Fish. Technical Paper No. 40 p.

Diaz, J. R. 2001. Overview of hypoxia around the world. Journal Environmental Quality 30(2):275–281.

Eby, L.A. and L.B. Crowder. 2002. Hypoxia-based habitat compression in the Neuse River estuary: context dependent shifts in behavioral avoidance thresholds. Canadian Journal of Fishery Aquatic Science 59:952–965.

Fonteneau, A. 1997. Atlas of tropical tuna fisheries. World catches and environment. ORSTOM editions. Paris Cedex, France, 192 p.

Goodyear, C.P. 2005. Atlantic blue marlin and yellowfin tuna: Comparative population vulnerability to fishing mortality. American Fishery Society Symposium 25:219–224.

Helly, J.J. and L.A. Levin. 2004. Global distribution of naturally occurring marine hypoxia on continental margins. Deep-Sea Research I, 51:1159–1168.

Prince, E.D. and C.P. Goodyear. 2006. Hypoxia-based habitat compression of tropical pelagic fishes. Fisheries Oceanography 15(6):451–464.

Sibert, J.R., and J.L. Nielsen, eds. 2001. Electronic Tagging and Tracking of Marine Fisheries. Kluwer Academic Publications Dordrecht, Netherlands, 468 p.

Stanley, D.R. and C.A. Wilson. 2004. Effect of hypoxia on the distribution of fishes around petroleum platforms off coastal Louisiana. North American Journal of Fishery Management 24:662–671.