Bull Mar Sci. 93(2):573–589. 2017
https://doi.org/10.5343/bms.2016.1008

research paper

Diurnal patterns in Gulf of Mexico epipelagic predator interactions with pelagic longline gear: implications for target species catch rates and bycatch mitigation

Eric S Orbesen [1*]
Derke Snodgrass [1]
Geoffrey S Shideler [2]
Craig A Brown [1]
John F Walter [1]

[1] *National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Drive, Miami, Florida 33149.*

[2] *University of Miami, Rosenstiel School of Marine & Atmospheric Science, 4600 Rickenbacker Causeway, Miami, Florida 33149.*

* *Corresponding author email: <eric.orbesen@noaa.gov>.*

ABSTRACT.—Bycatch in pelagic longline fisheries is of substantial international concern, and the mitigation of bycatch in the Gulf of Mexico has been considered as an option to help restore lost biomass following the 2010 Deepwater Horizon oil spill. The most effective bycatch mitigation measures operate upon a differential response between target and bycatch species, ideally maintaining target catch while minimizing bycatch. We investigated whether bycatch vs target catch rates varied between day and night sets for the United States pelagic longline fishery in the Gulf of Mexico by comparing the influence of diel time period and moon illumination on catch rates of 18 commonly caught species/species groups. A generalized linear model approach was used to account for operational and environmental covariates, including: year, season, water temperature, hook type, bait, and maximum hook depth. Time of day or moon phase was found to significantly alter catch rates for 88% of the taxa examined. Six taxa—swordfish (*Xiphias gladius* Linnaeus, 1758); tiger shark (*Galeocerdo cuvier* Péron and Lesueur, 1822); silky shark (*Carcharhinus falciformis* Müller and Henle, 1839); oilfish (*Ruvettus pretiosus* Cocco, 1833); bigeye thresher shark (*Alopias superciliosus* Lowe, 1841); and escolar (*Lepidocybium flavobrunneum* Smith, 1843)—exhibited higher catch rates at night, while eight taxa—skipjack tuna (*Katsuwonus pelamis* Linnaeus, 1758); wahoo (*Acanthocybium solandri* Cuvier, 1832); white marlin [*Kajikia albida* (Poey, 1860]; dolphinfish (*Coryphaena* sp.); yellowfin tuna (*Thunnus albacares* Bonnaterre, 1788); rays (*Pteroplatytrygon violacea* Bonaparte, 1832, *Mobulidae* sp.); lancetfish (*Alepisaurus* sp.), and blue marlin (*Makaira nigricans* Lacépède, 1802)—had higher daytime catch rates. These results reveal that shifts in effort between daytime and nighttime fishing (which are highly correlated with shifts between yellowfin tuna and swordfish targeting strategies) could have substantial, species-specific effects on bycatch rates. Whether driven by fishery conditions, market influences, or management measures, such temporal shifts in the timing of pelagic longline sets may have important implications for species-specific conservation goals and warrant further consideration.

Date Submitted: 5 May, 2016.
Date Accepted: 6 December, 2016.
Available Online: 18 January, 2017.

For over a century, pelagic longline (PLL) gear has been used throughout the world's oceans to target a variety of upper trophic level species, primarily tunas, swordfish (*Xiphias gladius* Linnaeus, 1758), pelagic sharks, and other pelagic teleosts (Shapiro 1950). Globally, the annual number of PLL hooks fished exceeds 1.4 billion, accounting for a substantial fraction of the world's tuna and swordfish production (Lewison et al. 2004a). One major issue faced in managing these fisheries is the bycatch of non-target species (Marín et al. 1998, Beerkircher et al. 2002, Lewison et al. 2004b). Regional fisheries management organizations (RFMOs) and individual nations have addressed these concerns through efforts to quantify bycatch by increasing onboard observer coverage and reporting, and enacting regulatory measures to specifically reduce bycatch interactions, as well as bycatch mortality (NOAA 2007). While these measures have helped to mitigate PLL bycatch, there is considerable sentiment that more substantial remedies are needed (Cox et al. 2007).

PLL fisheries operate in the oceanic pelagic environment, the largest habitat by volume on Earth. A defining characteristic of the pelagic zone is the diurnal vertical migration of zooplankton, fishes, crustaceans, and squids from the mesopelagic (200–1000 m) deep scattering layer (DSL) during the day to the epipelagic layer (<200 m) at night. Upper trophic level pelagic species have adapted their habitat use to exploit various aspects of this diurnal periodicity, developing specific life history adaptations that favor foraging in either low or high levels of available light (Brill 1994, Fritsches et al. 2003), corresponding to shallow or deeper depths (Brill 1994). Adaptations, such as brain and eye heaters (Carey 1982, Block 1987, Fritsches et al. 2005), facilitate foraging in lower temperatures, while visual abilities have adapted to foraging in high or low light levels (Warrant 1999, Horodysky et al. 2008). The combination of these adaptations and behavioral patterns result in differential utilization of the pelagic environment during day and night, and in turn, may correspond to differential vulnerability to capture by PLL gear.

Variable niche partitioning of the pelagic environment is clearly apparent in the diurnal habitat use of satellite-tracked upper trophic level predators. Swordfish (Dewar et al. 2011, Lerner et al. 2013), bigeye thresher shark (*Alopias superciliosus* Lowe, 1841) (Weng and Block 2004, Musyl et al. 2011), and escolar [*Lepidocybium flavobrunneum* (Smith, 1843)] (Kerstetter et al. 2008) have been observed to spend daytime hours in the mesopelagic zone (>500 m) and vertically migrate to the epipelagic zone (<75 m) at night. Yellowfin tuna [*Thunnus albacares* (Bonnaterre, 1788)] (Hoolihan et al. 2014, Weng et al. 2009), bigeye tuna [*Thunnus obesus* (Lowe, 1839)] (Arrizabalaga et al. 2008), blackfin tuna [*Thunnus atlanticus* (Lesson, 1831)] (Fenton et al. 2015), blue marlin (*Makaira nigricans* Lacépède, 1802) (Goodyear et al. 2008, Holland et al. 1990, Kerstetter et al. 2003), and white marlin [*Kajikia albida* (Poey, 1860)] (Hoolihan et al. 2015) have all been reported to reduce diving activity at night with a majority of the nighttime spent in near-surface waters, which could indicate a reduction in feeding at night for these species (Kerstetter and Graves 2006).

PLL fisheries routinely exploit behavioral differences by altering gear characteristics, location, fishing depth, and time of day for gear deployment to maximize catch rates of target species. These changes can also alter both the composition and magnitude of bycatch. Some examples of strategies employed by fishers include deploying hooks deeper in the water column (>400 m, Bigelow et al. 2006) when targeting bigeye tuna, and placing chemical light attractants near baits when targeting swordfish. Mitigation strategies that successfully reduce bycatch focus on gear or fishing modifications that reduce bycatch vulnerability. For example, Watson et al. (2005) found that hook type (circle vs J), as well as the bait it is paired with, can affect the catch rate and incidence of deep hooking for some sea turtle species, while maintaining similar catch rates of swordfish. Based primarily on the results of that study, the United States National Marine Fisheries Service (NMFS) enacted a rule mandating the use of circle hooks in the United States PLL fishery, banning the use of the J-style hook (Federal Register 2004). Gulf of Mexico (GOM) and Atlantic catches reported in the NMFS Pelagic Observer Program (POP) database were examined by Serafy et al. (2012), who found implementation of the rule resulted in a significantly higher survival (at boatside) rate for 10 out of 12 examined taxa. In addition to hook type, studies have found moon phase to be a significant factor in catch rate of both target and non-target species (e.g., Melvin et al. 2013, Shimose et al. 2013).

The GOM PLL fishery primarily targets yellowfin tuna and swordfish. While the gear used to target these species is similar, one major difference is the diel fishing period: swordfish PLL sets are generally allowed to soak (defined as the period of time after the last hook is deployed and before the first hook is retrieved) overnight, while yellowfin PLL sets soak during the daytime. It is likely that day and night catch rates vary for target and bycatch species; hence, a shift in effort between the fisheries could have a varied impact on bycatch species. The United States PLL fishery in the GOM currently operates under a wide variety of hook-type and bait-type restrictions as well as spatial and temporal closures (Walter 2015). As bycatch considerations remain a concern in this fishery and as options for restoring biomass lost following the Deepwater Horizon oil spill remain under consideration (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016), it is informative to evaluate potential options for bycatch reduction while supporting a viable fishery. The objectives of our study were to (1) examine the influence of diel period (day vs night) and moon illumination on catch per unit effort (CPUE) of 18 commonly caught taxa by the United States GOM PLL fishery, and (2) explore the potential implications to bycatch through diel shifts in effort.

Methods

Study and Data Selection Criterion

The United States PLL fishery operates year-round in broad areas of the western North Atlantic Ocean and GOM. A subset of vessels is required to have on-board trained NMFS observers to record specific data, including: date, set time and location, number of hooks, bait type, hook type, soak duration, set duration (the time between the first hook deployed and the last hook deployed), sea surface temperature (SST), and maximum estimated hook depth (NOAA 2014). Observers also record specific details on catch composition. An examination of the POP database (1998–2014) found that the only geographic region that had a sufficient sample size of both daytime and nighttime soaks was the Gulf of Mexico, so we restricted all subsequent analyses to this region (Fig. 1). To eliminate outliers, we removed atypical sets from our analyses using the following criteria: sets with fewer than 400 or more than 1400 hooks; a maximum hook depth (dropline length + gangion length + leader length) <15 fathoms; SST <10 °C; gear setting duration <1.5 or >6.5 hrs; a haul duration (the time between the first hook retrieved and the last hook retrieved) <2.5 or >10.5 hrs; soak duration <5 or >12 hrs; and any sets within the DeSoto Canyon, which has

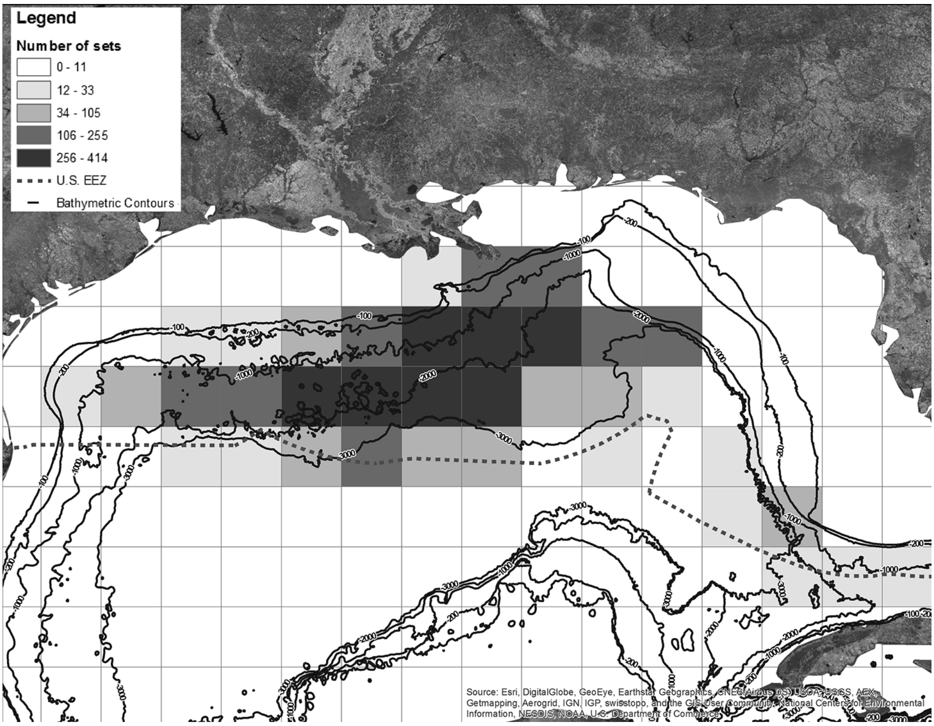

Figure 1. Map showing spatial extent of the current analysis. Plotting of individual longline set coordinates is prohibited for data confidentiality reasons; therefore, the density of sets is depicted at 1 degree resolution with red indicating the areas with the greatest density. Also included are bathymetric contours (black lines), and the boundary of the United States exclusive economic zone (dashed line).

been closed to commercial fishing since 2000 as part of the highly migratory species (HMS) longline bycatch reduction rule (Federal Register 2004).

We used the R package StreamMetabolism (Sefick 2015) to assign sunrise and sunset times, as well as the percent moon illumination for each set based on their dates and geographic coordinates. The additional focus on lunar illumination was to lend some biological inference into foraging behavior of different species as a function of light intensity rather than simply solar day and night.

PLL sets were divided into two major groups based on soak times. Sets that soaked between sunrise and sunset were defined as "day" sets, and sets that soaked between sunset and sunrise times were defined as "night" sets. When defining "day" and "night," we allowed for a diel overlap of up to 10% of the entire soak time. Sets exceeding a 10% diel overlap were excluded from further analysis.

Initial exploration of the relationship between catch in number and effort measured in either log(hooks per set) or log(hooks per set × hours fished) found no substantive relationship. For 10 of the species, the slope of the relationship between catch and log(hooks per set) was either 0 or negative. When the relationship was significant and positive (only the case for swordfish, yellowfin tuna, blackfin tuna, and bigeye tuna), the R^2 was extremely low, indicating a poor relationship. Similar patterns were observed for use of log(hooks per set × hours fished) as an effort measurement. As a result, so as to not impose an inappropriate relationship between catch and effort, we did not use hook effort as either a denominator—i.e., catch/effort—or as an offset in the analyses, and calculated CPUEs on a per set basis.

Species Assessed

An initial evaluation of all reported catch identified 18 species/species groups that had a sample size large enough (total positive sets >150) to allow for estimation of day/night differences. These 18 were separated into three groups: (1) target catch: yellowfin tuna and swordfish; (2) incidental catch: bigeye tuna; dolphinfish (*Coryphaena* sp.); escolar; and wahoo [*Acanthocybium solandri* (Cuvier, 1832)]; and (3) bycatch: blackfin tuna; skipjack tuna [*Katsuwonus pelamis* (Linnaeus, 1758)]; lancetfish [*Alepisaurus* sp.]; oilfish [*Ruvettus pretiosus* Cocco, 1833]; blue marlin; white marlin; bigeye thresher shark; silky shark [*Carcharhinus falciformis* (Müller and Henle, 1839)]; tiger shark (*Galeocerdo cuvier* Péron and Lesueur, 1822); great barracuda [*Sphyraena barracuda* (Edwards, 1771)]; rays [*Pteroplatytrygon violacea* (Bonaparte, 1832); *Mobulidae* sp.]; and pomfrets (*Bramidae* sp.).

Analyses and Catch Estimates

To test the null hypothesis of no influence of day vs night setting or moon phase on species-specific catch rates, we used a generalized linear model with a negative binomial distribution and no intercept, which included variables that would likely influence catch for each species. Using the Proc GLIMMIX function in SAS/STAT® software (SAS Institute Inc. 2008), the following model was applied independently to each species/species group:

$$\text{CPUE} = Y_i + S_j + H_k + T_l + B_m + M_n + C_o + D_p + M_n \times T_l$$

where CPUE = the number of fish of a given species/species group caught per set, Y_i the i^{th} year of set (i in 1998–2014), S_j the j^{th} season [j = 1 (December, January, February), 2 = (March, April, May), 3 = (June, July, August), 4 = (September, October, November)], H_k the k^{th} type of hook used (circle, J-hook, mix), T_l the l^{th} time of the day based on soak time (day, night), B_m the m^{th} bait type used (fish, squid, mix), M_n the n^{th} phase of the moon, categorized as the fraction of the moon illuminated (independent of day/night; M1 = 0–0.24, M2 = 0.25–0.49, M3 = 0.50–0.74, M4 = 0.75–1), C_o = sea surface temperature (°C), D_p = maximum hook depth (in water column, meters), and $M_n \times T_l$ = the interaction of the phase of the moon and the time of day. All factors were modeled as categorical factors except for sea surface temperature and hook depth.

To test for a "Time" (day vs night), "Moon", or "Time × Moon" effect on catch rates, least square means were generated independently on a species-specific basis. Statistical significance for model variables was assessed at $P < 0.05$.

Results

In total, 1865 day and 2975 night GOM PLL sets from 1998 to 2014 were analyzed, with the number of fish per taxon ranging from 163 (bigeye thresher shark) to 28,740 (yellowfin tuna).

The primary objective of our analysis was to test for a "Time," "Moon," or "Time × Moon" effect on catch rates after controlling for the potential influence of several environmental and operational variables. Although results were unique for each

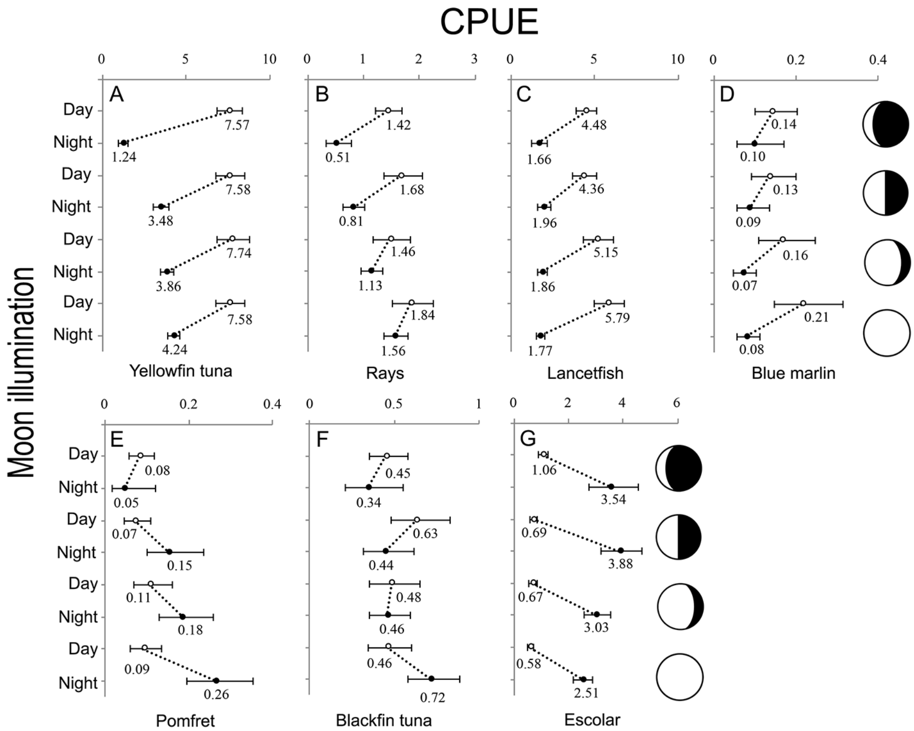

Figure 2. Catch per unit effort (set) for taxa for which time*moon was significant ($P < 0.05$). Shown are catch rates for day (white circles), night (black circles), and percentage of lunar illumination (from top to bottom: 0.00–0.24, 0.25–0.49, 0.50–0.74, 0.75–1.00). Horizontal lines indicate 95% confidence intervals. *X* axes are scaled to each individual species.

species, all had at least one of the independent model variables significantly affect catch rate (results of analysis of variance can be found for each species/species group in Online Appendix 1). With the exception of bigeye tuna and barracuda, all species had a significant effect of either Moon × Time (n = 7), Time (n = 6), or both Moon and Time (n = 3) (Table 1). For the majority of species, "Year," "Season," "Bait," and "Depth" were significant, whereas "Hook" was significant in only seven of the taxa (Table 1).

Catch Rate Estimates

Least squares mean catch rates were generated for each species for the main effects, Time and Moon, and the second order interaction, Moon × Time. The results are summarized below.

Moon × Time.—Four of the seven species with Moon × Time interaction effects [yellowfin tuna (Fig. 2A), rays (Fig. 2B), lancetfish (Fig. 2C), and blue marlin (Fig. 2D)] exhibited higher catch rates during the day for all four categories of moon illumination. While daytime catch rates exhibited little variance among the moon illumination categories, there was a >3-fold increase of catch for both yellowfin tuna and rays between the first and last moon categories [<25% (M1), >75% (M4)] at night. Escolar (Fig. 2G) exhibited significantly higher catch rates in each moon illumination

Table 1. Summary of catch per set for species (or species group) specific generalized linear model indicating the species and number of fish considered in each analysis. Statistical significance ($P < 0.05$) is indicated by asterisks. See text for model term descriptions, and see Online Appendix 1 for full model results.

Species	*n* (day / night)	Least squares means (day / night)	Year	Season	Hook	Bait	Temp	Depth	Time	Moon	Time × Moon
Yellowfin tuna	14,474 / 14,266	7.619 / 2.897	*	*		*	*	*	*	*	*
Swordfish	1,861 / 21,417	4.912 / 1.809	*	*	*	*	*	*	*	*	
Escolar	1,717 / 5,933	0.732 / 3.197	*	*		*	*	*	*	*	*
Wahoo	1,512 / 597	0.500 / 0.472		*	*	*	*		*	*	
Dolphin	5,712 / 2,334	0.076 / 0.296	*	*	*	*	*		*		
Bigeye tuna	126 / 567	0.066 / 0.099	*	*		*					
Pomfret	275 / 791	0.086 / 0.136	*	*			*	*	*	*	*
Rays	1,427 / 3,173	1.592 / 0.923	*	*	*	*	*		*	*	*
Skipjack	1,980 / 314	0.161 / 0.083	*	*		*	*		*	*	
Lancetfish	8,597 / 4,259	1.316 / 8.024	*	*	*	*	*	*	*		*
Blue marlin	605 / 538	0.455 / 0.077	*	*		*	*	*	*		*
Thresher shark	17 / 146	0.534 / 0.193		*					*		
White marlin	487 / 340	0.008 / 0.023	*		*	*	*	*	*		
Tiger shark	168 / 478	0.246 / 0.079	*	*		*		*	*		
Silky shark	234 / 1,173	0.049 / 0.111	*			*	*	*	*		
Oilfish	61 / 401	0.611 / 0.392	*	*	*	*	*	*	*		
Blackfin tuna	2,131 / 2,190	0.023 / 0.170	*	*		*	*			*	*
Barracuda	273 / 205	0.020 / 0.018	*	*		*	*	*			

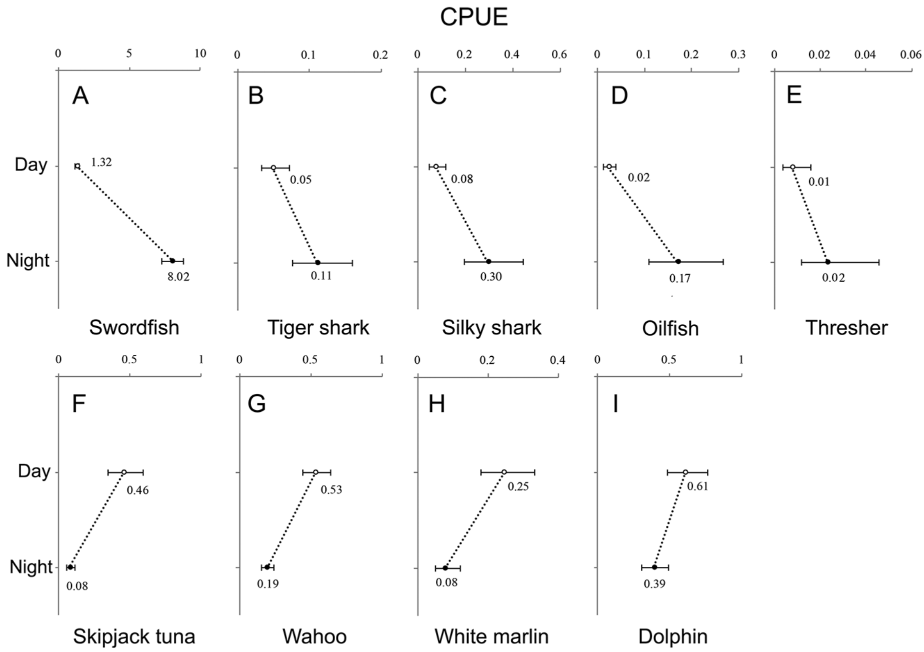

Figure 3. Catch per unit effort (set) for taxa that were significant ($P < 0.05$) for time and not significant for time*moon. Shown are catch rates for day (white circles), night (black circles). *X* axes are scaled to each individual species.

category during the night sets and had the highest catch rates during the first two moon illumination categories [<25% (M1), 25%–50% (M2)] for both day and night. Daytime catch rates for pomfrets were relatively unaffected by lunar illumination (Fig. 2E); however, there was a five-fold difference in catch rates between the first and last illumination categories [<25% (M1), >75% (M4)] at night. Daytime catches of blackfin tuna also did not appear to be affected by lunar illumination, (Fig. 2F); however, night catches doubled between the first and last illumination categories [<25% (M1), >75% (M4)].

Time.—Five species [swordfish (Fig. 3A), tiger shark (Fig. 3B), silky shark (Fig. 3C), oilfish (Fig. 3D), and bigeye thresher shark (Fig. 3E)] had a significantly higher catch rate during night sets. The greatest disparities were observed with oilfish and swordfish, which had 8.5 and 6 times higher catch rates at night, respectively. Four species [skipjack tuna (Fig. 3F), wahoo (Fig. 3G), white marlin (Fig. 3H), and dolphinfish (Fig. 3I)] all had higher catch rates during the day. Skipjack have the highest daytime catch rate relative to nighttime catch rate being 5.75 times higher during the day.

Moon.—Three species had a significant catch rate difference by moon illumination category, independent of time (Table 1). Swordfish exhibited highest catch rates during periods of low moon illumination [<25% (M1)] (Fig. 4A); skipjack tuna had the highest catch rates during periods with the greatest moon illumination [>50% (M3, M4)] (Fig. 4B). Catch rates for wahoo were lowest when the moon illumination was <25% (M1) and highest when the moon illumination exceeded 75% (M4) (Fig. 4C).

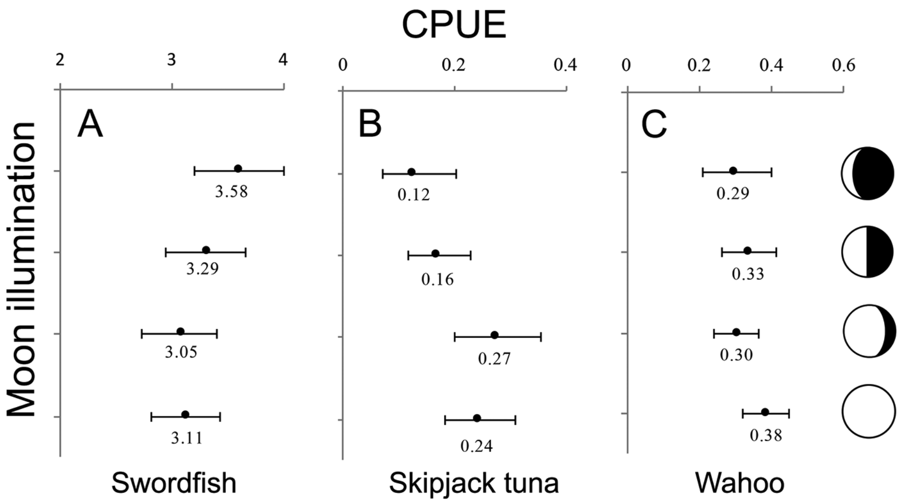

Figure 4. Catch per unit effort (set) for taxa that were significant ($P < 0.05$) for moon illumination, independent of time. Shown are catch rates for four moon illumination categories (from top to bottom: 0.00–0.24, 0.25–0.49, 0.50–0.74, 0.75–1.00). *X* axes are scaled to each individual species.

Discussion

Our study represents the first attempt to examine the effect of diel time period and moon phase on 18 commonly caught taxa in the GOM PLL fishery. Time of day or moon phase, and sometimes an interaction of the two, altered catch rates for the majority of the taxa examined (16 of 18). Seven of the taxa (swordfish, tiger shark, silky shark, oilfish, pomfrets, bigeye thresher shark, and escolar) exhibited significantly higher catch rates at night, while eight taxa (skipjack tuna, wahoo, white marlin, dolphin, yellowfin tuna, rays, lancetfish, and blue marlin) had significantly higher catch rates during the day (Fig. 5). The differential response between target and bycatch for day vs night sets indicates that there may be potential to alter target:bycatch ratios or to reduce bycatch of specific species by changing the time of day of setting. From 2010 to 2015, approximately 54% of GOM PLL sets were made during the day, with 46% of sets made at night. A shift in effort from day (generally yellowfin tuna targeted) to night (generally swordfish targeted) fishing would result, for example, in a reduction of catches of blue marlin and white marlin, two species which are currently classified as overfished by The International Commission for the Conservation of Atlantic Tunas (ICCAT). However, several species of conservation concern (e.g., some sharks and, and at least nominally, sea turtles) had higher catch rates at night.

The differential catch rates we found generally reflected the knowledge of the ecophysiology of each species with several notable exceptions (bigeye tuna and lancetfish), which are discussed below. The structure of eyes in pelagic fishes can vary greatly among species leading to differences in their visual acuity, especially at low light levels (Southwood et al. 2008), which could explain how the day vs night fisheries can have vastly different catch rates and species compositions. These differences are further reinforced by the interactions with moon illumination for several species such as yellowfin tuna and blue marlin, which are predominantly adapted to

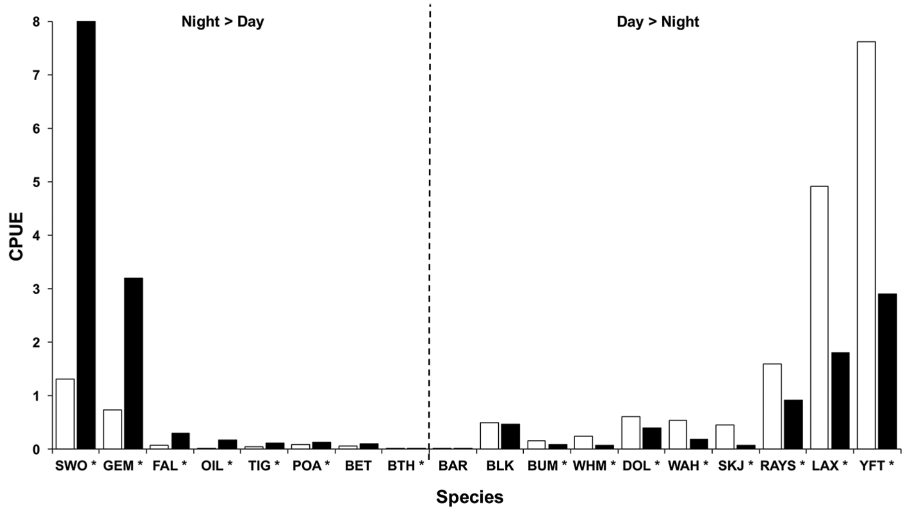

Figure 5. Relationship between catch per unit effort (number of fish per set) for day (white bars) and night (black bars) for swordfish (SWO), escolar (GEM), Silky shark (FAL), oilfish (oil), tiger shark (TIG), pomfrets (POA), bigeye tuna (BET), bigeye thresher shark (BTH), barracuda (BAR), blackfin tuna (BLK), blue marlin (BUM), white marlin (WHM), dolphin (DOL), wahoo (WAH), skipjack (SKJ), rays, lancetfish (LAX), and yellowfin tuna (YFT). Asterisks denote species exhibiting significant differences in diel catch rates ($P < 0.05$).

crepuscular and daytime feeding (Loew et al. 2002, Fritsches et al. 2003) but were found to maintain relatively high nighttime catch rates during higher moon illumination periods.

Target Catch

PLL fishers alter their methods based on the intended target species and, as expected, swordfish catches were significantly higher at night, while yellowfin tuna catches were significantly higher during the day. For swordfish, catch rates were highest during the period with the least lunar illumination, which is consistent with results reported by Poisson et al. (2010) in the Réunion Island PLL swordfish fishery. This result is of particular interest because most nighttime sets are made around the full moon (Fig. 6), which suggests that fishers expect higher catches during this period. However, lunar influence on catch is not consistent among fisheries and geographic regions. In the gillnet fisheries of Italy (Di Natale and Mangano 1995) and Turkey (Akyol 2013), CPUEs also tended to be higher during periods of low moon illumination, which was attributed to greater visibility of the net with increasing moon illumination. Four studies conducted in the central Atlantic PLL fishery (Draganik and Cholyst 1988), Portuguese PLL fishery (dos Santos and Garcia 2005), Hawaii PLL fishery (Bigelow et al. 1999), and the eastern Mediterranean Sea PLL fishery (Damalas et al. 2007) reported the highest catch rates around the full moon. Two studies conducted in the western North Atlantic PLL fishery (Podestá et al. 1993) and the Cuban artisanal fishery (Moreno et al. 1991) found no significant catch rate differences by moon phase.

Our results suggest that moon illumination has little impact on the catch rates of yellowfin tuna in the daytime fishery, however, lunar illumination has a much greater influence on catch for yellowfin tuna in the nighttime fishery, wherein catches rates

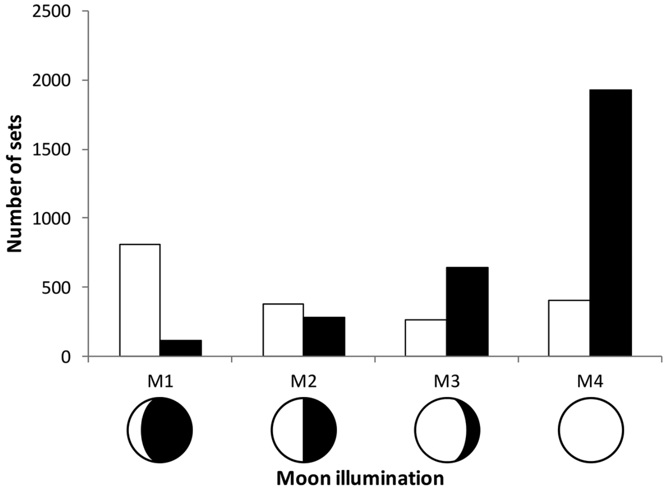

Figure 6. Distribution of daytime (white bars) and nighttime (black bars) sets used in the analysis by moon illumination categories (M1 = 0.00–0.24, M2 = 0.25–0.49, M3 = 0.50–0.74, M4 = 0.75–1).

are substantially lower during the M1 period. Conversely, night time swordfish catch rates are highest during the M1 period. Pallares and Garcia-Mamolar (1985) found catch rate differences for yellowfin tuna between waxing and waning moons with the highest catch rates in the second half of a waxing moon and the lowest catch rates in the first half of a waning moon. Lowry et al. (2007) reported highest catches for yellowfin tuna in the recreational fishery when moon illumination is <25%.

Incidental Catch

Incidental catch consists of a suite of species that, while not specifically targeted, are usually retained and have some economic importance. Two of the four incidental catch taxa (dolphinfish, wahoo) had consistently higher catches during the day, with wahoo also exhibiting a significant moon effect with highest catches occurring when moon illumination was >75% (M4, wahoo). The highest catch rates for escolar occurred at night when lunar illumination was <50%. Escolar are a benthopelagic fish that exhibit a nightly migration to near surface waters for feeding (Kerstetter et al. 2008), where they interact with longline gear. Escolar have large eyes and a low density of retinal ganglion cells, which give the fish a high optical sensitivity (Landgren et al. 2014); this might lead to lower catch rates during periods of greater lunar illumination due to an increase in the visibility of the gear. Similar to our results, Young et al. (2010) was unable to detect a day vs night hooking difference for bigeye tuna with PLL gear off eastern Australia; however, another study using hook timers in the western North Atlantic (Kerstetter and Graves 2006) reported that all 17 bigeye tuna captured were hooked at night. Evans et al (2008) suggests that the wide range of depths utilized by bigeye tuna allow for flexibility in foraging strategies. Geographic variability in prey behavior and abundance might result in area-specific differences in foraging strategies leading to the mixed results reported for diel catch rates of bigeye tuna.

Bycatch Species

It is important to understand that there are differential responses between target species and bycatch, and small shifts in fishing effort could have large impacts on catch rates of key bycatch species. Our results indicate that the bycatch (in numbers) was 1.7 times higher during the day; while conversely, the target catch (in numbers) was 1.3 times higher at night. The ratio of target to bycatch was 1:1.06 during the day and 1:0.49 at night, suggesting that a shift to nighttime fishing could result in a net reduction of the number of bycatch caught. A key objective of National Resource Damage Assessment restoration projects is to restore biomass after damages. After the Deepwater Horizon oil spill, there were very few restoration options for the pelagic environments, in contrast to littoral areas. The only projects in place are a reduction in PLL effort (to reduce catches of both target and bycatch species) and an initiative to shift fishing effort toward "greenstick" gear (a form of trolling), which has reduced incidences of bycatch (Deepwater Horizon Natural Resource Damage Assessment Trustees 2016). While a shift from day vs night PLL sets could be of restoration value in terms of reducing bycatch in numbers of fish, we recognize that the simple metrics of total (yellowfin tuna and swordfish) catch rate and total bycatch rate do not take into account the practicality, costs, and other indirect effects of shifting target species, or the relative conservation concerns among the various bycatch species. For example, some species are classified by the IUCN as near threatened, such as tiger sharks (Simpfendorfer 2009) and silky sharks (Bonfil et al. 2009), or vulnerable, such as bigeye thresher sharks (Amorim et al. 2009). In addition, while small sample sizes were prohibitive for modeling purposes, nominal catch rates of vulnerable and endangered sea turtles and bluefin tuna were greater at night.

Four taxa (lancetfish, blue marlin, white marlin, and rays) all had higher catch rates during the day and during the period of maximum lunar illumination. Skipjack also had higher catch rates during the day; however, the maximum catch rate was observed when moon illumination was between 50% and 75% (M3). Previous studies failed to detect a relationship between catch and lunar illumination for skipjack tuna (Kearney 1977, Pallares and Garcia-Mamolar 1985). Through the use of hook timers Berkeley and Edwards (1998) and Kerstetter and Graves (2006) reported that a majority of blue marlin were hooked during daylight hours, although sample sizes were low in both studies ($n < 14$). Sajeevan (2013) reported significantly higher catch rates for billfish during the full moon in the tuna directed PLL fishery around Andaman and Nicobar Islands; however, the author did not make a distinction between various billfish species. Shimose et al. (2013) also reported higher catch rates for blue marlin around the full moon in a recreational fishery; however, two other studies found no significant lunar effect (Nakamura and Rivas 1974, Lowry et al. 2007). Hazin et al. (2007) reported a weak relationship between catch rates and lunar illumination for both white and blue marlin. The variation in reported results for marlins suggests that the influence of diel periodicity and lunar illumination on catch rates may be specific to geographic regions.

With the exception of the target species, lancetfish had the highest daytime catch rate of any species examined. Even though lancetfish is a mesopelagic fish, a gut content comparison found that epipelagic prey dominated the diet of both lancetfish and yellowfin tuna, while the majority of swordfish diet consisted of mesopelagic prey (Potier et al. 2007) which could explain why lancetfish catch rates were highest on sets targeting yellowfin tuna. While the International Union for Conservation of

Nature lists lancetfish as a species of least concern (Paxton 2010), very little is known about their biology and an at vessel mortality rate of nearly 90% has been reported for the GOM PLL fishery (Serafy et al. 2012). In addition, lancetfish have very watery muscle tissue (Romanov and Zamorov 2002), and we have often observed hooks tearing free of fish upon gear retrieval (E Orbesen and D Snodgrass pers obs) likely resulting in underreported catches.

Catch rates for blackfin tuna were mixed across diel periods and lunar illumination with the highest catch rates occurring at night with lunar illumination exceeding 75% (M4), followed by daytime catches when lunar illumination is <50% (M1–M2). Using hook timers on PLL Kerstetter and Graves (2006) reported that 86% of blackfin were captured during the night, although the sample size was small (n = 7). These results suggest that the proportion of lunar illumination may be correlated with the distribution of foraging activities.

Conclusions and Further Research

Changes in regulations, market conditions, target species, and fleet composition can lead to shifts in the relative proportion of daytime and night time PLL sets. We found very strong differential catch rates between night and day for many species captured in the PLL fishery in the GOM. While the nighttime fishery had both the greatest targeted catch and the lowest associated bycatch, a shift of effort from day to night (or vice versa) would have mixed bycatch benefits. A shift of fishing activity from day to night would result in a significant numerical reduction of five bycatch species (white marlin, blue marlin, rays, skipjack tuna and lancetfish) with little impact on the target species catch rates, though it would switch the target from yellowfin tuna to swordfish. Swordfish catches would increase, helping the United States to meet its ICCAT allocated quota, though it might increase bycatch for several species of conservation concern. For example, a shift towards more night sets would increase bycatch of oilfish, pomfrets, silky shark, tiger shark, and bigeye thresher shark. Notably, we have only considered the catch rates in number due to the limitations of our data set. Catch rates in weight and by market category for target species would further elucidate the economic tradeoffs, which could lead to a temporal shift of effort. While our results clearly indicate that a differential response exists between night and day catch rates for target and bycatch species for this fishery, any consequences of an action that might shift effort between day vs night warrants continued exploration.

Further, certain bycatch species are of more immediate conservation concern than others, e.g., sharks (Gallagher et al. 2014) vs lancetfish (Paxton 2010). A shift in effort towards night fishing could increase vulnerability of three of the four elasmobranchs (silky shark, tiger shark, and bigeye thresher shark) relative to both of the billfish species (white and blue marlin). While a shift to nighttime fishing might have an overall reduction in the catch rates of the bycatch species we examined, the differential and taxa-specific responses indicate that a shift in fishing effort warrants an examination of the anticipated impact in light of conservation concerns for the affected species. It is also worth highlighting that some taxa such as sea turtles, marine mammals, bluefin tuna, and some of the rarer elasmobranchs were so numerically rare in the observer data set that they could not be included in the modeling. As these species may be of the highest conservation concern, their potential day/night vulnerability to longline fishing should be evaluated further.

Acknowledgments

We thank all of the observers who have collected data for the SEFSC Pelagic Observer Program used in the present study. This research was supported by the US National Marine Fisheries Service.

Literature Cited

Akyol O. 2013. The influence of the moon phase on the CPUEs of swordfish gillnet fishery in the Aegean Sea, Turkey. Turk J Fish Aquat Sci. 2:355–358.

Amorim A, Baum J, Cailliet GM, Clò S, Clarke SC, Fergusson I, Gonzalez M, Macias D, Mancini P, Mancusi C, Myers R, Reardon M, Trejo T, Vacchi M, Valenti SV. 2009. *Alopias superciliosus*. The IUCN Red List of Threatened Species 2009: eT161696A5482468. Accessed 24 February, 2016. http://dx.doi.org/10.2305/IUCN.UK.2009-2.RLTS.T161696A5482468.en

Arrizabalaga H, Pereira J, Royer F, Galuardi B, Goni N, Artetxe I, Arregi I, Lutcavage M. 2008. Bigeye tuna (*Thunnus obesus*) vertical movements in the Azores Islands determined with pop-up satellite archival tags. Fish Oceanogr. 17:74–83. http://dx.doi.org/10.1111/j.1365-2419.2008.00464.x

Beerkircher LR, Cortés E, Shivji M. 2002. Characteristics of shark bycatch observed on pelagic longlines off the southeastern United States, 1992–2000. Mar Fish Rev. 64:40–49.

Berkeley SA, Edwards RE. 1998. Factors affecting billfish capture and survival in longline fisheries: potential application for reducing bycatch mortality. ICCAT Col Vol Sci Pap. 48(1):255–262.

Bigelow KA, Boggs CH, He X. 1999. Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. Fish Oceanogr. 8:178–198. http://dx.doi.org/10.1046/j.1365-2419.1999.00105.x

Bigelow K, Musyl MK, Poisson F, Klieber P. 2006. Pelagic longline gear depth and shoaling. Fish Res. 77:173–183. http://dx.doi.org/10.1016/j.fishres.2005.10.010

Block BA. 1987. Billfish brain and eye heater: a new look at nonshivering heat production. News Physiol Sci. 2:208.

Bonfil, R, Amorim A, Anderson C, Arauz R, Baum J, Clarke SC, Graham RT, Gonzalez M, Jolón M, Kyne PM, et al. 2009. *Carcharhinus falciformis*. The IUCN Red List of Threatened Species 2009: e.T39370A10183906. Accessed 24 February, 2016. http://dx.doi.org/10.2305/IUCN.UK.2016-3.RLTS.T39370A2909465.en

Brill RW. 1994. A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. Fish Oceanogr. 3:204–216. http://dx.doi.org/10.1111/j.1365-2419.1994.tb00098.x

Carey FG. 1982. A brain heater in the swordfish. Science. 216:1327–1329. http://dx.doi.org/10.1126/science.7079766

Cox TM, Lewison RL, Žydelis R, Crowder LB, Safina C, Read AJ. 2007. Comparing effectiveness of experimental and implemented bycatch reduction measures: the ideal and the real. Conserv Biol. 21(5):1155–1164. http://dx.doi.org/10.1111/j.1523-1739.2007.00772.x

Damalas D, Megalofonou P, Apostolopoulou M. 2007. Environmental, spatial, temporal and operational effects on swordfish (*Xiphias gladius*) catch rates of eastern Mediterranean Sea longline fisheries. Fish Res. 84:233–246. http://dx.doi.org/10.1016/j.fishres.2006.11.001

Deepwater Horizon Natural Resource Damage Assessment Trustees. 2016. Deepwater Horizon oil spill: Final Programmatic Damage Assessment and Restoration Plan and Final Programmatic Environmental Impact Statement. Available from: http://www.gulfspillrestoration.noaa.gov/restoration-planning/gulf-plan

Dewar H, Prince ED, Musyl MK, Brill RW, Sepulveda C, Luo J, Foley D, Orbesen ES, Domeier ML, Nasby-Lucas NI, et al. 2011. Movements and behaviors of swordfish in the Atlantic and Pacific oceans examined using pop-up satellite archival tags. Fish Oceanogr. 20(3):219–241. http://dx.doi.org/10.1111/j.1365-2419.2011.00581.x di Natale A, Mangano A. 1995. Moon phases influence on CPUE: a first analysis of swordfish driftnet catch data from the Italian fleet between 1990 and 1991. ICCAT Col Vol Sci Pap. 44(1):264–267.

dos Santos MN, Garcia A. 2005. The influence of the moon phase on the CPUEs for the Portuguese swordfish (*Xiphias gladius* L., 1758) fishery. ICCAT Col Vol Sci Pap. 58(4):1466–1469.

Draganik B, Cholyst J. 1988. Temperature and moonlight as stimulators for feeding activity by swordfish. ICCAT Col Vol Sci Pap. 27(1):305–314.

Evans K, Langley A, Clear NP, Williams P, Patterson T, Sibert J, Hampton J, Gunn JS. 2008. Behaviour and habitat preferences of bigeye tuna (*Thunnus obesus*) and their influence on longline fishery catches in the western Coral Sea. Can J Fish Aquat Sci. 65:2427–2443. http://dx.doi.org/10.1139/F08-148

Federal Register. 2004. Atlantic highly migratory species (HMS): pelagic longline fishery; final rule. 69:40,734–40,758.

Fenton J, Ellis JM, Falterman B, Kerstetter DW. 2015. Habitat utilization of blackfin tuna, Thunnus atlanticus, in the north-central Gulf of Mexico. Environ Biol Fishes. 98(4):1141–1150. http://dx.doi.org/10.1007/s10641-014-0347-3

Fritsches KA, Marshall NJ, Warrant EJ. 2003. Retinal specializations in the blue marlin: eyes designed for sensitivity to low light levels. Mar Freshwat Res. 54:333–341. http://dx.doi.org/10.1071/MF02126

Fritsches KA, Brill RW, Warrant EJ. 2005. Warm eyes provide superior vision in swordfishes. Curr Biol. 15:55–58. http://dx.doi.org/10.1016/j.cub.2004.12.064

Gallagher A, Orbesen ES, Hammerschlag N, Serafy JE. 2014. Vulnerability of oceanic sharks as pelagic longline bycatch. Glob Ecol Conserv. 1:50–59. http://dx.doi.org/10.1016/j.gecco.2014.06.003

Goodyear CP, Luo J, Prince ED, Hoolihan JP, Snodgrass D, Orbesen ES, Serafy JE. 2008. Vertical habitat use of Atlantic blue marlin *Makaira nigricans:* interaction with pelagic longline gear. Mar Ecol Prog Ser. 365:233–245. https://doi.org/10.3354/meps07505

Hazin FHV, Hazin HG, Travassos P, Oliveira I. 2007. Standardized catch per unit of effort of white marlin, *Tetrapturus albidus*, and blue marlin, *Makaira nigricans*, caught by Brazilian commercial tuna longline fleet. ICCAT Col Vol Sci Pap. 60:1652–1662.

Holland K, Brill R, Chang RKC. 1990. Horizontal and vertical movements of Pacific blue marlin captured and released using sportfishing gear. Fish Bull. 88:397–402.

Hoolihan JP, Wells RJD, Luo J, Falterman B, Prince ED, Rooker JR. 2014. Vertical and horizontal movements of yellowfin tuna in the Gulf of Mexico. Mar Coast Fish. 6:211–222. http://dx.doi.org/10.1080/19425120.2014.935900

Hoolihan JP, Luo J, Snodgrass D, Orbesen ES, Barse AM, Prince ED. 2015. Vertical and horizontal habitat use by white marlin *Kajikia albida* (Poey, 1860) in the western North Atlantic Ocean. ICES J Mar Sci. http://dx.doi.org/10.1093/icesjms/fsv082

Horodysky AZ, Brill RW, Warrant EJ, Musick JA, Latour RJ. 2008. Comparative visual function in five sciaenid fishes inhabiting Chesapeake Bay. J Exp Biol. 211:3601–3612. http://dx.doi.org/10.1242/jeb.023358

Kearney RE. 1977. An estimation of Papua New Guinea's tuna fisheries potential. Commission du Pacifique Sud, document occasionnel N° 3, Nouméa, Nouvelle-Calédonie, mai 1977.

Kerstetter DW, Luckhurst BE, Prince ED, Graves JE. 2003. Use of pop-up satellite archival tags to demonstrate survival of blue marlin (*Makaira nigricans*) released from pelagic longline gear. Fish Bull. 101:939–948.

Kerstetter DW, Graves JE. 2006. Effects of circle versus J-style hooks on target and non-target species in a pelagic longline fishery. Fish Res. 80:239–250. http://dx.doi.org/10.1016/j.fishres.2006.03.032

Kerstetter DW, Rice PH, Snodgrass D, Prince ED. 2008. Behavior of an escolar *Lepidocybium flavobrunneum* in the windward passage as determined by popup satellite archival tagging. Gulf Caribb Res. 20:97–102. http://dx.doi.org/10.18785/gcr.2001.14

Landgren E, Fritsches K, Brill R, Warrant E. 2014. The visual ecology of a deep-sea fish, the escolar *Lepidocybium flavobrunneum* (Smith, 1843). Philos Trans Roy Soc B. 369:20130039. http://dx.doi.org/10.1098/rstb.2013.0039

Lerner JD, Kerstetter DW, Prince ED, Talaue-McManus L, Orbesen ES, Mariano A, Snodgrass D, Thomas GL. 2013. Swordfish vertical distribution and habitat use in relation to diel and lunar cycles in the western North Atlantic. Trans Am Fish Soc. 142(1):95–104. http://dx.doi.org/10.1080/00028487.2012.720629

Lewison RL, Freeman SA, Crowder LB. 2004a. Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. Ecol Lett. 7:221–231. http://dx.doi.org/10.1111/j.1461-0248.2004.00573.x

Lewison RL, Crowder LB, Read AJ, Freeman SA. 2004b. Understanding impacts of fisheries bycatch on marine megafauna. Trends Ecol Evol. 19:598–604. http://dx.doi.org/10.1016/j.tree.2004.09.004

Loew ER, McFarland WN, Margulies D. 2002. Developmental changes in the visual pigments of the yellowfin tuna, *Thunnus albacares.* Mar Freshwat Behav Physiol. 35:235–246. http://dx.doi.org/10.1080/10236240210000003826

Lowry M, Williams D, Metti Y. 2007. Lunar landings—relationship between lunar phase and catch rates from an Australian gamefish-tournament fishery. Fish Res. 88:15–23. http://dx.doi.org/10.1016/j.fishres.2007.07.011

Marín Y, Brum F, Barea LC, Chocca JF. 1998. Incidental catch associated with swordfish longline fisheries in the south-west Atlantic Ocean. Mar Freshwat Res. 49:633–639. http://dx.doi.org/10.1071/MF97243

Melvin EF, Guy TJ, Read LB. 2013. Reducing seabird bycatch in the South African joint venture tuna fishery using bird-scaring lines, branch line weighting and nighttime setting of hooks. Fish Res. 147:72–82. http://dx.doi.org/10.1016/j.fishres.2013.04.015

Moreno S, Pol J, Munoz L. 1991. Influencia de la luna en el abundancia del emperador. ICCAT Col Vol Sci Pap. 35(2):508–510.

Musyl MK, Brill RW, Curran DS, Fragoso NM, McNaughton LM, Nielsen A, Kikkawa BS, Moyes CD. 2011. Postrelease survival, vertical and horizontal movements, and thermal habitats of five species of pelagic sharks in the central Pacific Ocean. Fish Bull. 109:341–368.

Nakamura E, Rivas LR. 1974. An analysis of the sportfishery for billfishes in the northeastern Gulf of Mexico during 1971. *In:* Proceedings of the International Billfish Symposium Kailua-Kona, Hawaii, 9–12 August, 1972, Part 2. NOAA Technical Report. NMFS. 675:269–289.

NOAA (National Oceanic and Atmospheric Administration). 2007. Magnuson–Stevens Fishery Conservation and Management Act. Public Law 94-265 as amended by the Magnuson–Stevens Fishery Conservation and Management Reauthorization Act (P.L. 109-479):176.

NOAA (National Oceanic and Atmospheric Administration). 2014. Pelgacic Observer Training Manual. Accessed 1 March, 2016. Available from: http://www.sefsc.noaa.gov/fisheries/observers/forms.htm

Pallares P, Garcia-Mamolar JM. 1985. Efectos de las fases de la luna sobre los rendimientos de la flota atunera-tropical española. ICCAT Col Vol Sci Pap. 23:228–236.

Paxton JR. 2010. *Alepisaurus ferox.* The IUCN Red List of Threatened Species 2010: e.T154820A4641606. Accessed 24 February, 2016. http://dx.doi.org/10.2305/IUCN.UK.2010-4.RLTS.T154820A4641606.en

Podestá GP, Browder JA, Hoey JJ. 1993. Exploring the association between swordfish catch rates and thermal fronts on United States longline grounds in the western north Atlantic. Cont Shelf Res. 13:253–277. http://dx.doi.org/10.1016/0278-4343(93)90109-B

Poisson F, Gaertner JC, Taquet M, Durbec JC, Bigelow K. 2010. Effects of lunar cycle and fishing operations on longline-caught pelagic fish: fishing performance, capture time, and survival of fish. Fish Bull. 108:268–281.

Potier M, Marsac F, Cherel Y, Lucas V, Sabatié R, Maury O, Ménard F. 2007. Forage fauna in the diet of three large pelagic fishes (lancetfish, swordfish and yellowfin tuna) in the western equatorial Indian Ocean. Fish Res. 83:60–72. http://dx.doi.org/10.1016/j.fishres.2006.08.020

Romanov EV, Zamorov VV. 2002. First record of a yellowfin tuna (*Thunnus albacares*) from the stomach of a longnose lancetfish (*Alepisaurus ferox*). Fish Bull. 100(2):386–389.

Sajeevan MK. 2013. Evaluation of the effect of lunar cycle, monsoon and spatial differences on billfishes. IOTC. 2013:WPB-11–WPB-20. Available from: http://www.iotc.org/sites/default/files/documents/2014/01/IOTC-2013-WPB11-20.pdf

SAS Institute Inc. 2008. SAS/STAT® 9.2 User's Guide. Cary, NC: SAS Institute Inc.

Sefick S Jr. 2015. StreamMetabolism - a package for calculating single station metabolism from diurnal oxygen curves. R package version 1.1.1. Available from: http://CRAN.R-project.org/package=StreamMetabolism

Serafy JE, Orbesen ES, Snodgrass DJG, Beerkircher LR, Walter JF. 2012. Hooking survival of fishes captured by the United States Atlantic pelagic longline fishery: impact of the 2004 circle hook rule. Bull Mar Sci. 88(3):605–621. http://dx.doi.org/10.5343/bms.2011.1080

Shimose T, Yokawa K, Tachihara K. 2013. Higher catch rates around the full moon for blue marlin, *Makaira nigricans*, in a diurnal trolling fishery. Bull Mar Sci. 89:759–765. http://dx.doi.org/10.5343/bms.2012.1094

Shapiro S. 1950. The Japanese long-line fishery for tunas. Comm Fish Rev. 12(4):1–26.

Simpfendorfer C. 2009. *Galeocerdo cuvier*. The IUCN Red List of Threatened Species 2009: e.T39378A10220026. Accessed 24 February, 2016. http://dx.doi.org/10.2305/IUCN.UK.2009-2.RLTS.T39378A10220026.en

Southwood A, Fritsches K, Brill R, Swimmer Y. 2008. Sound, chemical, and light detection in sea turtles and pelagic fishes: sensory-based approaches to bycatch reduction in longline fisheries. Endanger Species Res. 5:225–238. http://dx.doi.org/10.3354/esr00097

Walter J. 2015. Update of standardized catch rates of large bluefin tuna (*Thunnus thynnus*) from the U.S. pelagic longline fishery in the Gulf of Mexico 1987-2013 with correction for weak hook effects. Collect Vol Sci Pap ICCAT. 71(3):1260–1278.

Warrant EJ. 1999. Seeing better at night: life style, eye design and the optimum strategy of spatial and temporal summation. Vision Res. 39:1611–1630. http://dx.doi.org/10.1016/S0042-6989(98)00262-4

Watson JW, Epperly SP, Shah AK, Foster DG. 2005. Fishing methods to reduce sea turtle mortality associated with pelagic longlines. Can J Fish Aquat Sci. 62:965–981. http://dx.doi.org/10.1139/f05-004

Weng KC, Stokesbury MJ, Boustany AM, Seitz AC, Teo SL, Miller SK, Block BA. 2009. Habitat and behaviour of yellowfin tuna *Thunnus albacares* in the Gulf of Mexico determined using pop-up satellite archival tags. J Fish Biol. 74(7):1434–1449. http://dx.doi.org/10.1111/j.1095-8649.2009.02209.x

Weng K, Block B. 2004. Diel vertical migration of the bigeye thresher shark (*Alopias superciliosus*), a species possessing orbital retia mirabilia. Fish Bull. 102:221–229.

Young JW, Lansdell MJ, Cooper SP, Campbell RA, Juanes F, Guest MA. 2010. Feeding ecology and niche segregation in oceanic top predators off eastern Australia. Mar Biol. 157:2347–2368. http://dx.doi.org/10.1007/s00227-010-1500-y