Effects of lunar cycle and fishing operations on longline-caught pelagic fish: fishing performance, capture time, and survival of fish

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Abstract—Commercial longline fishing data were analyzed and experiments were conducted with gear equipped with hook timers and time-depth recorders in the Réunion Island fishery (21°5′S lat., 53°28′E long.) to elucidate direct and indirect effects of the lunar cycle and other operational factors that affect catch rates, catch composition, fish behavior, capture time, and fish survival. Logbook data from 1998 through 2000, comprising 2009 sets, indicated that swordfish (*Xiphias gladius*) catch-per unit of effort (CPUE) increased during the first and last quarter of the lunar phase, whereas albacore (*Thunnus alalunga*) CPUE was highest during the full moon. Swordfish were caught rapidly after the longline was set and, like bigeye tuna (*Thunnus obesus*), they were caught during days characterized by a weak lunar illumination—mainly during low tide. We found a significant but very low influence of chemical lightsticks on CPUE and catch composition. At the time the longline was retrieved, six of the 11 species in the study had >40% survival. Hook timers indicated that only 8.4% of the swordfish were alive after 8 hours of capture, and two shark species (blue shark [*Prionace glauca*] and oceanic whitetip shark [*Carcharhinus longimanus*]) showed a greater resilience to capture: 29.3% and 23.5% were alive after 8 hours, respectively. Our results have implications for current fishing practices and we comment on the possibilities of modifying fishing strategies in order to reduce operational costs, bycatch, loss of target fish at sea, and detrimental impacts on the environment.

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Empirical studies have shown that surface longlines set at night are more productive for capturing swordfish (*Xiphias gladius*) than longlines set during the day (Kume and Joseph, 1969). Studies with ultrasonic telemetry have proved useful for understanding habitat distribution and for providing some insights into short-term horizontal and vertical movements of swordfish (Carey and Robinson, 1981; Carey, 1990). Recently, more advanced tagging technology devices, such as archival tags (Takahashi et al., 2003) and pop-up satellite archival tags (Canese et al., 2008; Neilson et al., 2009), have provided comprehensive information on the diel behavior of swordfish and their movement patterns, both of which indicate the ability of swordfish to navigate to long distance feeding areas in the Pacific and Atlantic oceans and Mediterranean Sea. Vertical movement data obtained from these various studies have shown diel diving patterns to be very consistent, as have been observed in other pelagic fishes (Musyl et al., 2003). During the daytime, swordfish can spend most of their time at depths between 250 and 650 m (Canese et al., 2008) and as deep as 900 m (Takahashi et al., 2003). At crepuscular hours, they swim up and down through a considerable range of depths following the movements of organisms in the deep sound-scattering layers but restrict their movements to forage in the uniform surface mixed-layer during the night. They also feed during the day and can demonstrate basking behavior. Carey and Robinson (1981) suggested that swordfish swimming activity in the water column is closely associated with prey locations and concluded that lunar illumination was a determining factor influencing vertical migrations. Swordfish are "strike and return" feeders (Nakamura, 1983) targeting fast-moving prey. Swordfish can achieve a maximum speed of

130 km/h (Lee et al., 2009) and Fritsches et al. (2005) demonstrated that their large eyes and pupils are ideally adapted to detect rapid movements in dim light. Swordfish rely on visual cues at small scales (meters) and ambient light conditions are likely to be a major factor influencing feeding behavior.

There is strong anecdotal information from captains who target large pelagic fish that the lunar phase affects fishing success for swordfish and other pelagic fish. The effect of the lunar cycle on swordfish catchability has been investigated in longline (Bigelow et al., 1999; Neves Dos Santos and Garcia, 2005; Damalas et al., 2007) and driftnet fisheries (Di Natale and Mangano, 1995), but the results obtained are not directly comparable because they were conducted in different areas and fisheries. Generalized additive models (GAMs) have been used to examine the relative influence of environmental conditions and operational factors on pelagic longline catch rates (Bigelow et al., 1999; Walsh and Kleiber, 2001; Tserpes et al., 2008). In the case of the Réunion Island longline fishery, Guyomard et al. (2004) demonstrated significant effects (among others) of geostrophic currents generated by sea level anomalies (SLA) and lunar day on swordfish catch and catch per unit of effort (CPUE, number of fish per 1000 hooks).

I n 1991, the first swordfish longliner began operating from Réunion Island, a French overseas territory in the southwestern Indian Ocean (21°5′S lat., 53°28′E long.), Two main factors promoted the development of this fishery: 1) the success of the Asian fleet that was based at Réunion Island and 2) a new tax regulation, offering exemption for certain investments in French overseas territory, which encouraged French fishing companies to come to Réunion Island. The annual average catch in the Réunion Island longline fishery during the years 1996–2000 was 2670 metric tons (t) and the composition by weight was 1730 t (65%) of swordfish (*Xiphias gladius*), 320 t (12%) of albacore (*Thunnus alalunga*), 270 t (10%) of yellowfin tuna (*T. albacares*), 130 t (5%) of bigeye tuna (*T. obesus*), 90 t (3%) of billfish (Indo-Pacific black marlin [*Makaira indica*], Indo-Pacific blue marlin [*M. mazara*], shortbill spearfish [*Tetrapturus angustirostris*], and Indo-Pacific sailfish [*Istiophorus platypterus]),* 60 t (2%) of sharks, and 70 t (3%) of other species.

The main goal of the current study was to investigate the performance of the domestic longline fishery at Réunion Island with regard to several variables to determine whether lunar periodicity affected the catch of pelagic species. A three-year logbook data series (1998–2000) was used. In addition, data were augmented by deploying time-depth recorders (TDRs) and hook-time recorders on a number of commercial longline sets. Information on capture time from hook timers allowed us to investigate the survival of large pelagic fish on longlines. Hourly catch rates were correlated with lunar illumination but also with the tidal phase which could be considered as an indicator of induced local currents.

Finally, to test the assumption that feeding behavior of large pelagic fish was predicated on vision (swordfish can differentiate between blue-green wavelengths [Fritsches et al., 2005]), we investigated whether green chemical lightsticks influenced catch rates and species composition. With the combined results for catch rates and species composition, we comment on the possibilities of modifying fishing operations and strategy 1) to reduce operational costs during fishing trips, 2) to reduce loss of target fish at sea, and 3) to reduce bycatch mortality in accordance with the United Nations guidelines for responsible fisheries (FAO, 2003).

Materials and methods

Operational characteristics of the domestic longline fleet

The Réunion Island swordfish longline fishery is a surface fishery. An adapted "American style" gear is used, where the monofilament mainline (3.5–4 mm in diameter) longline is set at dusk and fished during the night. The mainline was deployed from a hydraulically powered spool over the stern and fishing depth was controlled by adjusting branchline (~20 m) and floatline lengths (~10–90m), distance between buoys (~50 m), number of hooks between floats (6–10 hooks), and vessel speed (Fig. 1). In strong currents, lead weights can also be added to branchlines to control mainline depth. The fishery uses J hooks (size 8/0 or 9/0) baited with squid *(Illex* spp.) and green chemical lightsticks were attached ~1 m above the hook on every third branchline.

The domestic longline fleet can be categorized by two vessel sizes (classes): a small-medium boat class (vessels <16 m), and a large boat class (vessels ≥16 m). The fishery underwent dramatic changes between 1992 and 2000 expanding from 5 to 23 active small-medium boats and from zero to 9 large boats, the latter with a peak of 14 in 1998. No longliners were authorized to fish within a zone of 30 nautical miles (~55 km) from Réunion Island in order to avoid conflicts with the artisanal tuna fishery. Thus, these vessels explored new fishing areas within and beyond the French Exclusive Economic Zone (EEZ) (Fig. 2). The number of days at sea varied according to vessel size, vessel capacity, and weather conditions. The smallest boats stayed at sea 2–3 days, medium-size vessels generally stayed 6–8 days; whereas some of the largest vessels stayed at sea for up to 30 days. The large boats gradually expanded to fishing grounds to the west and southwest of Réunion Island within the EEZ in association with deep seamounts and sea surface temperature (SST) fronts (Fig. 2; area C) and to the Mozambique Channel (area B) and to Seychelles Island waters in 1997 and 1998 (area A). A decline of large boats from the fleet brought notable changes; therefore catches in 1999 and in 2000 were taken mainly around Réunion Island between 20º and 25ºS lat. and 50°–60°E long. Only a few vessels ventured far from Réunion Island in 2000. Table 1 summarizes

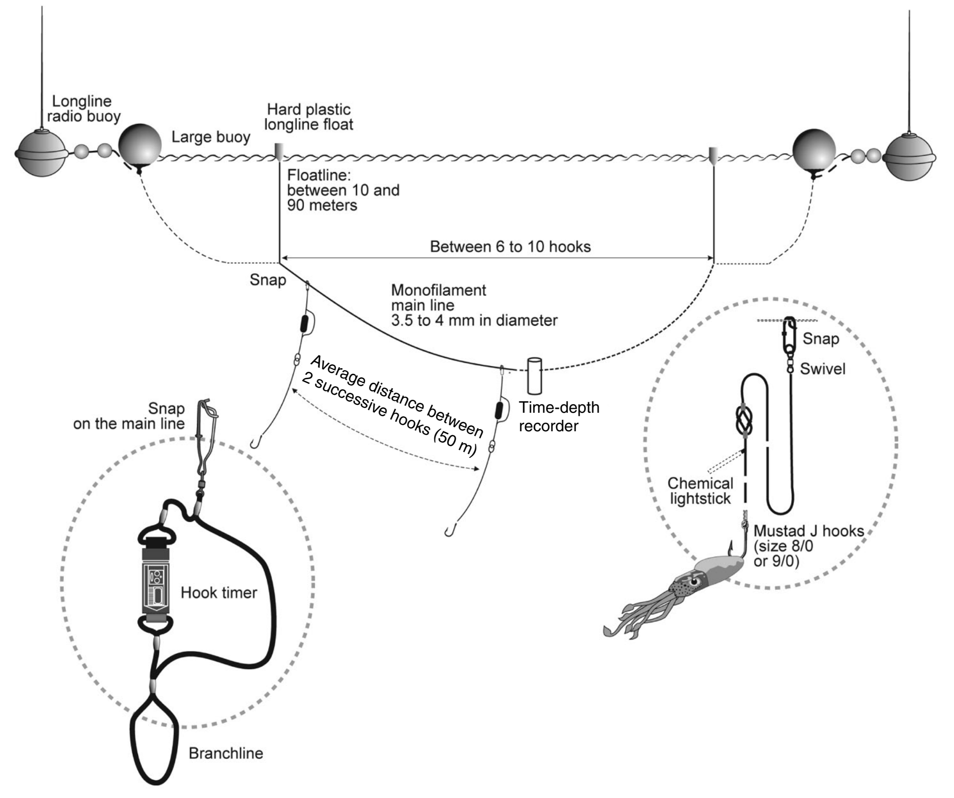

Figure 1

Longline gear used in the domestic Réunion Island longline fishery: hook timers, time-depth recorders, and chemical lightsticks. Experiments were conducted off the island between June 1998 and November 2000.

the fishery and environmental indices and subsequent statistical analyses.

Logbook (database 1)

During the "Programme Palangre Réunion" (PPR), a rigorous data-collecting strategy was implemented. Logbooks were distributed to all domestic vessels, along with species identification guides, including guides for identifying sharks and sea turtles. Because these logbooks were completed on a voluntary basis, logbook data were cross checked against landing receipts to estimate the monthly logbook coverage. Logbook data made up the major source of information used to analyze the effect of operational and gear-setting practices on catches.

Analyses focused on data collected between 1998 and 2000 and which encompassed several lunar cycles. Logbook submission was high by the domestic fleet and the fleet operated between 20° and 23°S lat. and 53° and 57° long. (Fig. 2, area D). Database 1 consisted of 2009 longline sets where seven species were easily identified: albacore, bigeye and yellowfin tuna, dolphinfish, swordfish, blue (*Prionace glauca*) and oceanic whitetip sharks (*Carcharhinus longimanus*), and three broader shark species groups (mako sharks [*Isurus* spp.], hammerhead sharks [*Sphyrna* spp.], and other sharks grouped together as "mixed sharks").

Experimental fishing (databases 2 and 3)

Fish behavior on a daily scale (fine scale) was investigated on portions of the longlines equipped with hook timers to estimate fish capture time and with time-depth recorders (TDRs) attached in the middle position between two consecutive floats, which is theoretically the deepest point reached by the mainline. On 160 sets, 284 TDRs were used to estimate hook depth (TDR depth+branchline length). The number of hook timers deployed per set varied from 61 to 408 according to the boat size and weather conditions. For thirty-three trips, 28,974 hook timers were used during 160 sets. These experimental data constituted database 2. The time between the setting of the hook and capture time was represented as a capture index and stratified into four classes (0–4 h, 4–7 h, 7–10 h and >10 h). Database 3 represented other longline field trials where CPUE and catch compositions were compared by using gear with various densities of chemical lightsticks.

Environment (database 4)

Database 4 consisted of two environmental databases that were linked to experimental databases to investigate cyclical lunar influence on CPUE. Lunar days were coded in chronological order with values between 1 and 30. A lunar phase index was allocated to each fishing day according to the four phases of the moon (new moon, first quarter, full moon, and last quarter). Full and new moons refer to the day of each full or new moon ±2 days. Lunar illumination was calculated for each fish caught, according to its hooking hour, based on the angle of elevation of the moon (on a 24-h cycle). These data were obtained by using an astronomical software package called LunarPhase (http://www.nightskyobserver.com/LunarPhase/index.htm, accessed January 2000) and were stratified into three classes: 1) angle <45° (low illumination); 2) high illumination (angle >45°–90°); and 3) dark (new moon). An important underlying assumption inherent in this approach is that the cloud coverage is not considered when calculating the index. An index for tidal phase was assigned to each hooking time and location by the French Service Hydrographique et Oceanographique de la Marine (SHOM). The tidal index consisted of four nominal phases (ebb, high, flood, and low) and is thus a good approximation of the theoretical sea level height changes, although it does not account for current velocity. The fishery operates throughout the year and no temporal discontinuities in fishing effort were evident because effort was quite homogeneous for indices of lunar illumination and tide phase.

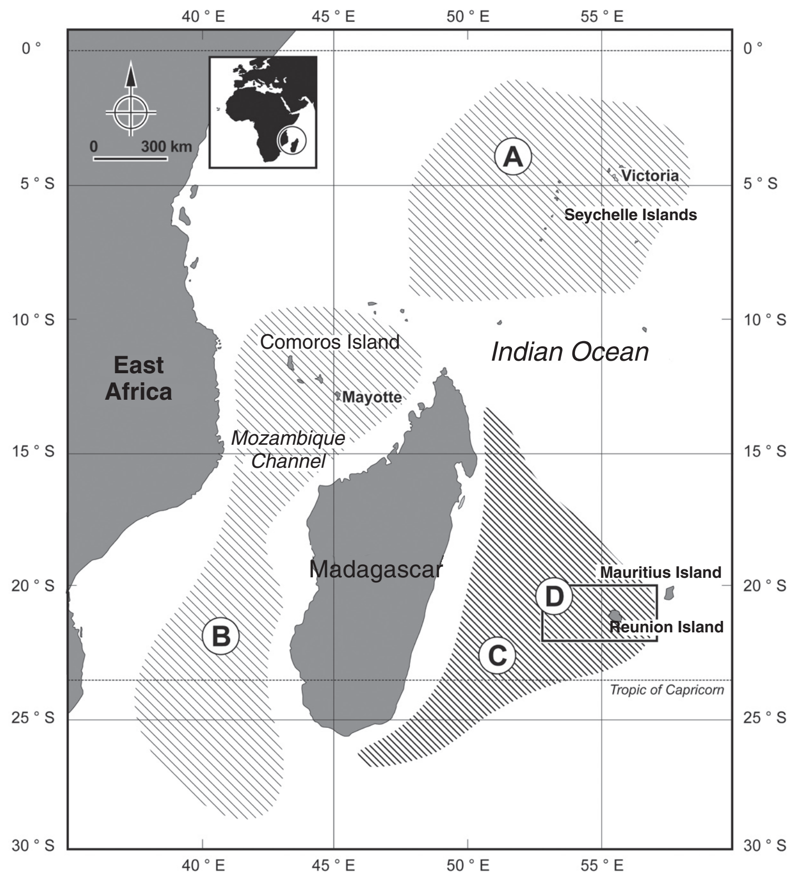

Figure 2

Location of Réunion Island in the southwestern Indian Ocean. The areas shown with diagonal lines are the three fishing grounds of the fleet between 1998 and 2000, the Seychelle waters (area A), the Mozambique Channel (area B), the west and southwest of Réunion Island within the EEZ in association with deep seamounts and sea surface temperature (SST) fronts (area C). Logbook data used to analyse the effect of operational and gear setting practices on catches where located in area D (20°–23°S lat. and 53°–57°E long.)

Statistical methods

Lunar effect on fishing performance was investigated at two different scales. At a larger scale, we conducted a between-class analysis (Dolédec and Chessel, 1990, 1994; Gaertner et al., 2005; Bigot et al., 2008) in order to approximate the influence of lunar days (phase) on the CPUE of all the species recorded in logbooks (database 1), where "lunar days" was a categorical factor. For that purpose, we sought axes for the between-group analysis that would best discriminate the centers of gravity of each lunar day and allow us to investigate associations between lunar phases and the variability of CPUE for each species. In addition, a permutation test, which extended the test of Romesburg (1985) to all kinds of variables (Manly, 1991), was carried out to test the significance of the between-group variability. We used nonparametric LOESS regression to further investigate variability in CPUE for species that were most affected by the lunar day. On a finer scale, we carried out a multiple correspondence analysis (MCA)—equivalent to normalized principal component analysis (PCA) to determine the most favourable catch factors on a daily scale (Tenenhaus and Young, 1985; Mazouni et al., 1996). MCA allowed us to visualize the associations between each of the five major species caught during experimental sets and three lunar-related factors studied on a daily scale (tide phase, capture time, lunar illumination).

A between-group centered principal component analysis (CPCA, R-mode) and a between-group factorial correspondence analysis (FCA) were conducted to examine the influence of lightstick density on CPUE and catch composition of experimental sets (database 3). The ADE-4 software (Thioulouse et al., 1997, http//pbil.

Table 1

Variables, indices, and types of analyses performed during our study to elucidate the direct and indirect effects of lunar cycle and other operational factors affecting fishing performance, fish behavior, capture time, and fish survival for the domestic Réunion Island longline fishery.

Database	Scale	Variable	Index	Type of analyses
1 Logbook	Set (day)	Number of fish (7 species, 3 broad groups) number of hooks	CPUE (number of fish per 1000 hooks)	Between classes analysis, Permutation test, Nonparametric loess regression
2 Experiments with hook timers (HT)	Hook (hour)	Setting time Capture time	Elapsed time after setting as capture time index (0–4 h, 4–7 h, 7–10 h, and >10 h)	Multiple correspondence analysis
3 Experiments with lightsticks	Set (day)	Number of fish (7 species, 3 broad groups) Number of hooks Lightstick density	Lightstick density and CPUE	Centered principal component analysis (CPCA)
			Catch composition (percentage of fish per species	Factorial correspondence analysis (FCA)
4 Environmental	Set (day)	Lunar day	Lunar day (1 to 30) and lunar phase index (new moon, first quarter, full moon, last quarter)	
	Hook (hour)	Angle of elevation of the moon tide characteristics	Lunar illumination index: low illumination intensity (angle <45°), high illumination intensity angle (45°–90°) and dark (new moon)	
			Tide phase index (ebb, high, flood and low)	

univ-lyon1.fr/ADE-4, accessed January 2000) was used to perform calculations and graphical displays for between-group analyses.

Results

Effect of the moon at a large scale

Time series covered by logbook data The CPCA indicated that lunar day represented only 13.3% of the total variability, although the influence of the lunar day on CPUE was highly significant (permutation test, $P<0.01$). The first two axes explained 71% and 17% of the between-lunar-day variability and illustrated the effect of lunar days on CPUE (Fig. 3). Albacore CPUE reached maximum values during the full moon (between the 13th and 19th day of the lunar cycle), whereas CPUE was less important during the new moon (between the 25th and 6th day of the lunar cycle).

Swordfish was the unique component of the second axis (Fig. 3) and the projection of lunar days on this axis indicated that the highest CPUE occurred mainly during two short periods of time within the lunar cycle, between the 7th and 9th day and between the 23rd and 26th day. None of the other four species analyzed appeared to be affected by the lunar day (Fig. 3).

Case study of albacore and swordfish For albacore, LOESS regression confirmed that the highest CPUE was obtained during the full moon (Fig. 4A). In contrast, there was no apparent influence of tidal fluctuation (Fig. 4C). The situation for swordfish was more complex. Variation of CPUE according to lunar cycle provided less contrast than that for albacore. LOESS regression confirmed that the highest CPUE was obtained during the first and last quarter of the moon as characterized by the lowest tidal ranges. Nevertheless, the relationship between swordfish CPUE and lunar intensity was not consistent because the CPUE progressively decreased during the last days of the last quarter and reached the lowest values around the full moon phase (Fig. 4B). Moreover, CPUE decreased as tidal amplitude increased. Large confidence intervals around the mean CPUE pertaining to the new moon indicated a higher variability in fishing performance during this phase. The lowest CPUE was recorded between the 14th and 17th day of the lunar cycle during the full moon (which is characterized by the largest tidal ranges and maximum lunar illumination).

Effect of lunar luminescence, tidal phase, and tidal velocity of local induced currents on catches

Sample sizes of five species were considered adequate to conduct detailed analyses of lunar-related variables on a fine scale, although 15 species and 2 broader species groups were identified in the catches (Table 2). Swordfish were caught rapidly after the gear was set (Fig. 5) and during days characterized by weak lunar illumination because most of the individuals were confined in an area corresponding simultaneously to the negative part of both axes (Fig. 6). The occurrence of swordfish on the negative side of the first axis and mainly on the negative axis of the second axis indicates that swordfish were caught during low tides and to a lesser extent during flood tides characterized by a low current. These results reinforce earlier conclusions obtained at a large scale, although the results from the experimental data were weaker than the data from logbooks.

As with swordfish, bigeye tuna are likely to be caught rapidly after the gear is set during periods of weak lunar illumination (Figs. 5 and 6). Bigeye tuna and blue shark exhibited an opposite distribution on the second axis, which indicated that blue sharks were caught late during the soak time of the longline set and when luminescence was minimal. The limited number of albacore and yellowfin caught in the experimental data may have restricted the statistical analysis. No particular favorable or unfavorable conditions were identified for albacore on a daily scale (Fig. 6), in contrast to the influence of lunar intensity observed on a monthly scale.

Effect of chemical lightsticks

A marginally significant influence of lightstick density on CPUE and catch composition was observed (permutation tests, $P<0.05$); but the majority of the CPUE variability was not correlated with lightstick density (93.6% for PCA and 91.3% for FCA, Table 3).

Capture depths, times, and fish survival

TDRs indicated that the deepest depth of the mainline was 110 m; most of the longlines were deployed between 30 and 110 meters (Fig. 7); consequently most hooks fished between 50 and 130 meters. Hook timers indicated that the number of commercial species caught (swordfish and tunas) declined with soak time (i.e., with the time the gear was in the water [Fig. 5A]) and indicated an opposite trend for five bycatch species (Fig. 5B). Blue marlin and dolphinfish were mostly caught after the longline had soaked for 8 hours or longer. In particular, pelagic stingrays, and sailfish to a lesser extent, were caught mostly during gear retrieval. In contrast, more than 60% of the sharks were caught within the initial seven hours of fishing.

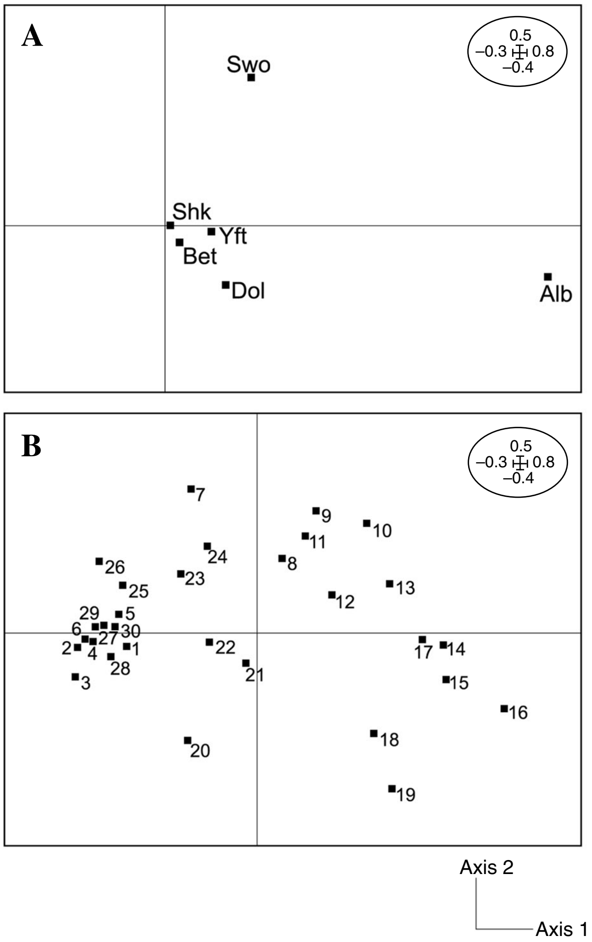

Figure 3

A between-group projection of (**A**) the species, and of (**B**) the lunar days of the month (represented as numbers between 1 to 30), on the first plane of the between-group centered principal component analysis (CPCA) conducted on catch per unit of effort of albacore (Alb, *Thunnus alalunga*); swordfish (Swo; *Xiphias gladius*); bigeye tuna (Bet, *Thunnus obesus*); yellowfin tuna (Yft, *Thunnus albacares*); sharks (Shk), and dolphinfish (Dol, *Coryphaena hippurus*). Scale box in the upper right corner of each plot indicates the limits for the first and second axes.

Fish survival at longline retrieval varied widely among species (Table 4). Survival was high for species such as dolphinfish and black marlin which strike the hooks mainly during retrieval. Over 40% of the main elasmobranch species (blue shark, oceanic whitetip, and pelagic stingray), as well as sailfish, were alive upon retrieval. Among commercially important species, 49% of the bigeye tuna were alive upon retrieval, whereas only 3 of 79 albacore were alive. Swordfish survival was also low (20%) and no relationship was evident between fish size and mortality. Bigeye tuna and two shark species exhibited the highest survival when the longline was at a settled depth. Six species (represented by sample sizes >30 individuals) exhibited long survival times of up to 14 hours after capture (Table 4).

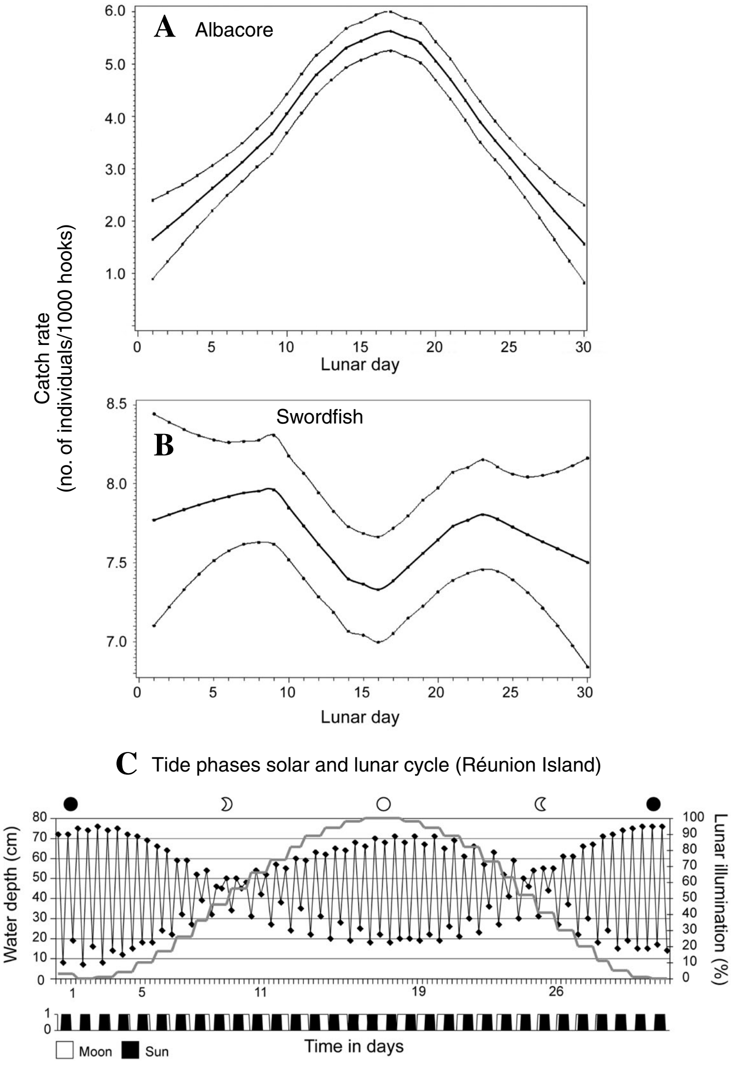

Figure 4

Variation of the mean catch per unit of effort (and 95% confidence intervals) of (**A**) albacore (*Thunnus alalunga*), and (**B**) swordfish (*Xiphias gladius*) per lunar day determined with a nonparametric regression method (LOESS) between 1998 and 2000. Tidal ranges and lunar luminescence during a complete lunar cycle are illustrated in (**C**).

Discussion

Lunar illumination and sensory abilities of large pelagic fish

At a broad scale, our results indicate that the phases of the moon, which presumably affect ambient light levels, have a significant but limited influence on the night catch rates of albacore and swordfish in the Réunion Island-based swordfish longline fishery, whereas such a lunar influence was not found for other species. We found that the highest swordfish CPUE occurred during the first and last quarters of the lunar cycle—a finding that is consistent with the results obtained for the same fishery in the Indian Ocean (Guyomard et al., 2004).

Other studies conducted in various geographical areas with distinctive oceanic features, have indicated that lunar influences on swordfish CPUE are not consistent. The highest swordfish CPUE occurred during the full moon phase in the Hawaii-based swordfish fishery (Bigelow et al., 1999) and in the central Atlantic swordfish fishery (Draganik and Cholyst, 1988). In the U.S. longline fishery in the western Atlantic, more hooks were deployed in the 2-week period around full moon, but Podesta et al. (1993) could not demonstrate a significant correlation between CPUE and lunar illumination, whereas Hazin et al. (2002) and Damalas et al. (2007) showed positive effects of other lunar phases on swordfish CPUE. No significant relationship between lunar phase and swordfish abundance could be demonstrated in artisanal swordfish fisheries off the Cuban coast (Moreno et al., 1991). In the case of a swordfish gillnet fishery operating in the Mediterranean Sea, Di Natale and Mangano (1995) showed that the lowest catch rate occurred during the full moon. Lastly, it is apparent that swordfish size and maturity may confound catch rates during different lunar phases (Draganik and Cholyst, 1988; Neves Dos Santos and Garcia, 2005).

One possible explanation for the absence of a consistent pattern in association with lunar phase could be attributed to prey availability. In the Atlantic Ocean, swordfish appear to exhibit feeding plasticity (i.e., are opportunistic feeders and exhibit various search strategies for prey) based on forage abundance and prey size; larger swordfish tend to eat larger prey than smaller swordfish (Chancollon et al., 2006). In the Pacific Ocean, Young et al. (2006) showed no significant relation-

Table 2

Number and percentage of catch per species during experimental sets conducted from commercial vessels in the domestic Réunion Island-based longline fishery between June 1998 and November 2000.

Common name	Species	Number of individuals	Percentage
Swordfish	*Xiphias gladius*	389	47.8
Blue shark	*Prionace glauca*	92	11.3
Bigeye tuna	*Thunnus obesus*	86	10.6
Albacore	*Thunnus alalunga*	79	9.7
Yellowfin tuna	*Thunnus albacares*	66	8.1
Common dolphinfish	*Coryphaena hippurus*	48	5.9
Oceanic whitetip shark	*Carcharhinus longimanus*	17	2.1
Pelagic stingray	*Pteroplatytrygon violacea*	12	1.5
Indo-Pacific sailfish	*Istiophorus platypterus*	7	0.9
Hammerhead sharks	*Sphyrna* spp.	4	0.5
Indo-Pacific black marlin	*Makaira indica*	3	0.4
Escolar	*Lepidocybium flavobrunneum*	3	0.4
Indo-Pacific blue marlin	*Makaira mazara*	2	0.2
Wahoo	*Acanthocybium solandri*	2	0.2
Shortfin mako shark	*Isurus oxyrinchus*	2	0.2
Barracuda	*Sphyraena* spp.	1	0.1
Leatherback turtle	*Dermochelys coriacea*	1	0.1
Total hook timers triggered		2115	
Hook timers triggered with catch		814	
Hook timers triggered without catch		1301	

Table 3

Decomposition of inertia between and within groups according to the lightstick density factor for centered principal component analysis (CPCA), factorial correspondence analysis (FCA), and associated permutation tests.

	Between lightstick density CPCA	Between lightstick density AFC
Total inertia	$3.234\ 10^{2}$	1.597
Between groups	$2.046\ 10^{1}$ (6.32%)	$1.391\ 10^{-1}$ (8.7%)
Within groups	$3.030\ 10^{2}$ (93.68%)	1.458 (91.3%)
Permutation test	$P<0.05$	$P<0.05$

ship between prey biomass and lunar phase but found that prey size significantly increased with swordfish size and that this increase coincided with a dietary shift from fish to cephalopods (Palko et al., 1981). This finding indicates that swordfish have the ability to forage at considerable depth and temperature, which are afforded by a suite of physiological adaptations to enable opportunistic feeding within the deep sound-scattering layer (DSL) (Josse et al., 1999; Musyl et al., 2003), Gilly et al. (2006) depicted lunar influence on the vertical migration of squid, which, in turn, would have a direct effect on the distribution and vulnerability of swordfish.

We found that higher swordfish CPUE correlated with small tides. Moreover, at a finer scale, we found that higher swordfish CPUE occurred with lower tidal fluctuations which coincided with the possible generation of low-velocity oceanic currents. These results were consistent with the results obtained when applying GAMs on similar scales (Guyomard et al., 2004), where the meridional component (V) of geostrophic currents derived from sea level anomaly (SLA) data was the most significant environmental factor within one of the models tested. It was likely that the low positive V values (i.e., low velocity currents to the north) were more beneficial for catch rates, whereas the trend became clearly negative for higher velocity values.

We assumed that the influence of the tide and associated local current velocities would be complex and affect the dispersion of organisms within the DSL and other associated organisms of the mixed layer. In addition, current could affect turbidity by advecting organisms and particulate matter and alter the shape and depth obtained by the longline (Bigelow et al., 2006). To gain insights into swordfish behavior during complex patterns of current velocities, acoustic telemetry could be used to provide short-term horizontal movement data that could help in elucidating the effect of the tide on the foraging behavior of large pelagic fish. Analysis

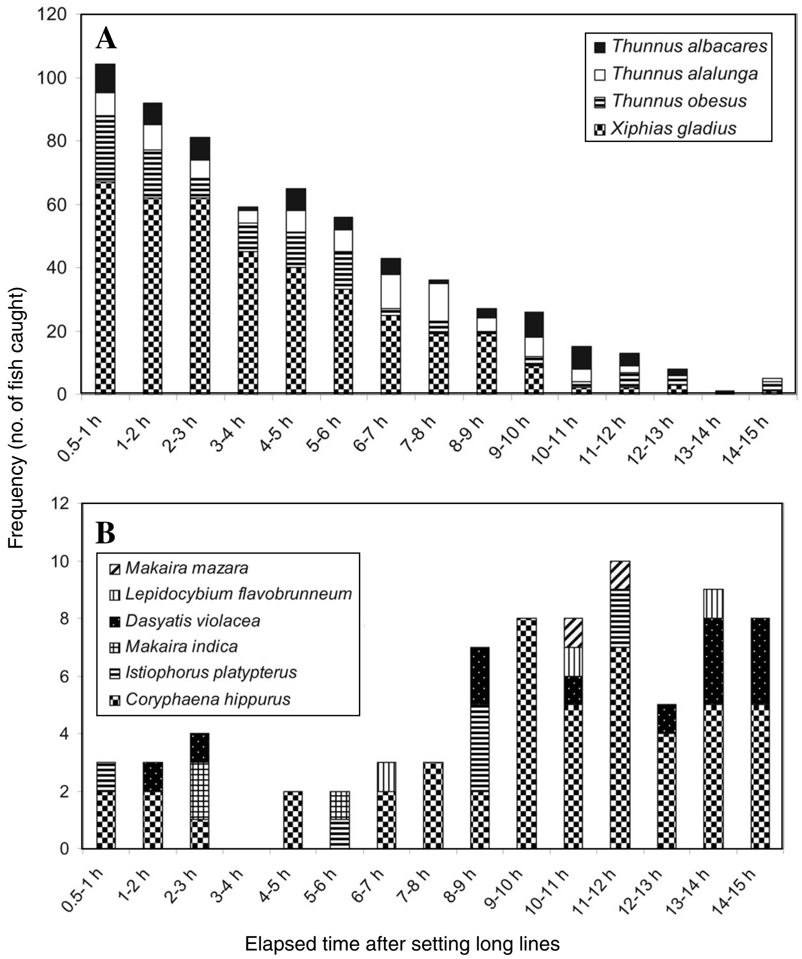

Figure 5

Hook-timer data for 10 species caught on longlines (n=284) in the domestic Réunion Island fishery between June 1998 and November 2000. Height of each bar represents the sum of frequencies for (**A**) the main commercial species and for (**B**) billfish and other bycatch species.

of the trajectories on a finer scale would help in elucidating the foraging behavior in three dimensions. Thus, using acoustic tracks, Brill et al. (1993) presented evidence for passive, current-borne movements (which tended to drift in the prevailing current) for striped marlin around the Island of Hawaii.

Our results revealed that swordfish were caught on days characterized by a weak lunar illumination. It is likely that increased illumination may alter the diving behavior of swordfish in near-surface waters. Ortega-Garcia et al. (2008) stated that vulnerability to gillnets was reduced because of better visibility during the full moon phase whereby swordfish could presumably detect and therefore avoid the net. As a logical extension, we could hypothesize that this visual avoidance could also apply to longline gear. In constrast, albacore exhibited higher CPUE during the full moon, which indicates increased foraging during the time of prey availability. This result supports that of Pusineri et al. (2008), who found that the composition of the diet of pelagic predators in the northeast Atlantic differs considerably in terms of species composition and prey size.

Blue shark, the major shark found in bycatch of tuna and swordfish longline fisheries worldwide (Bonfil, 1994; Gilman et al., 2008) exhibited catch rates that correlated strongly with soak time but were not significantly influenced by lunar effects. To our knowledge, studies of the possible effect of lunar illumination on CPUE are rare for blue shark and virtually nonexistent for albacore and yellowfin tuna because these species are mainly caught during the day by Asian distant-water longline fleets. Our results agree with those of Bigelow et al. (1999), who showed that the effect of the moon phase appeared insignificant on blue shark CPUE. Blue shark are opportunistic feeders that are probably at-

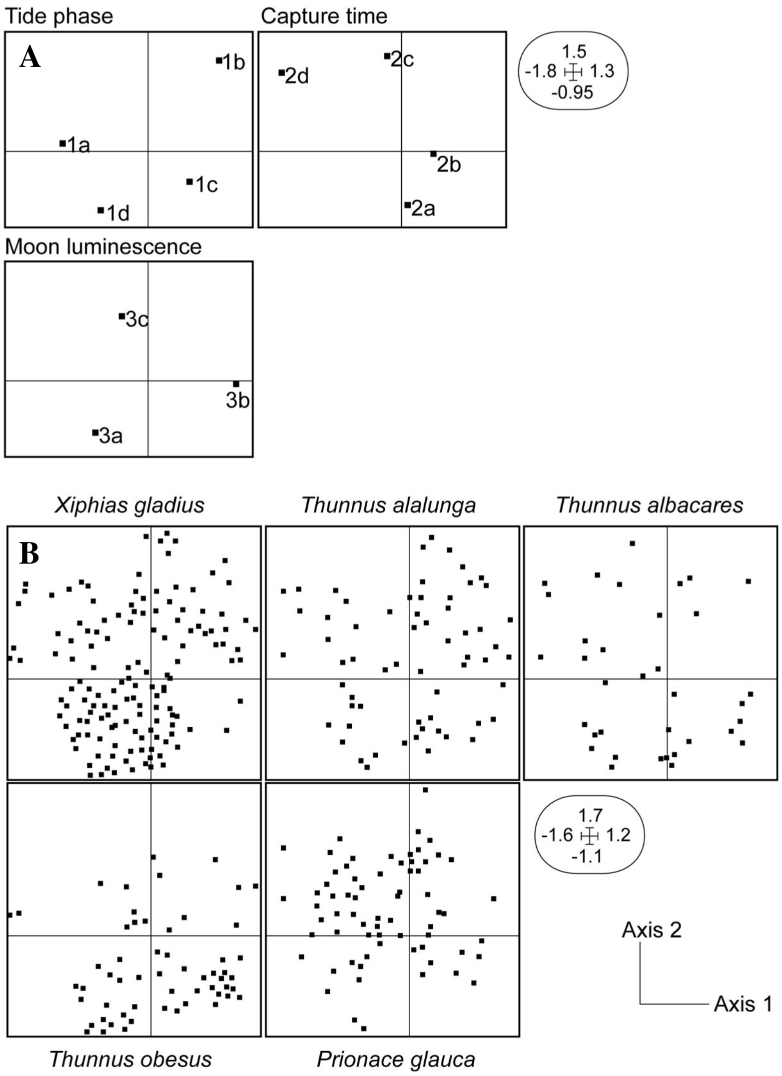

Figure 6

(**A**) Projection of the modalities for each factor on all species combined, and (**B**) the projection of individual fish stratified by species on the first axis of the multiple correspondence analyses (MCA). Description of the index modalities: "tide phase" 1a=ebb; 1b=high, 1c=flood, and 1d=low; "capture time" 2a=0–4 h, 2b=4–7 h, 2c=7–10 h, and 2d=>10 h; "moon luminescence index" 3a=low, 3b=high, and 3c=dark

tracted by offal and spent bait discarded during the haul but also by the distress signals of captured fish (Myrberg et al., 1969)

Our results indicate that swordfish and bigeye tuna exhibit active predation when lunar illumination is weak. These results are consistent with the findings of Fristches et al. (2005), who showed that retinas of swordfish and bigeye tuna provide visual acuity and sensitivity to blue-green light and thus these apex predators are efficient visual hunters in dim light.

We found that 60% to 80% of swordfish were caught after the gear soaked 4–6 hours and these results indicated a possible positive effect of bait freshness on the attractiveness of bait to swordfish and bigeye tuna. The effect of the chemical lightsticks on catch rate also decreased with time and as their glowing intensity waned. The role of the lightsticks is still not clear, although it is thought that they either attract predators to the bait or they attract small fish and squid (Hazin et al., 2005), or both, and as such, were considered as an important refinement of the longline gear. A significant but low association of lightstick density on CPUE was confirmed by our analyses. Bigelow et al. (1999) found that increasing the proportion of lightsticks from

Table 4

Number of fish caught per species (No.), number of fish alive at time of hauling (*no.*), range of size per species (lower jaw fork length for billfish and swordfish, and fork length for other species in cm), maximum survival time per species, percentage of individuals alive at time of hauling, and percentage alive eight hours after hooking.

Common name	Species	No.	*no.*	Length (cm)	Maximum survival time (hours)	Alive at time of hauling (%)	Alive after 8 hours (%)
Swordfish	*Xiphias gladius*	389	76	93–242	14	19.5	8.4
Bigeye tuna	*Thunnus obesus*	86	42	65–160	14	48.8	26.7
Albacore	*Thunnus alalunga*	79	3	105–113	8	3.8	1.2
Yellowfin tuna	*Thunnus albacares*	66	23	99–150	14	34.8	13.6
Common dolphinfish	*Coryphaena hippurus*	48	32	83–120	14	66.7	8.3
Oceanic whitetip shark	*Carcharhinus longimanus*	17	7	120–151	14	41.1	23.5
Blue shark	*Prionace glauca*	92	45	150–240	14	48.9	29.3
Indo-Pacific sailfish	*Istiophorus platypterus*	7	3	?–163	4	42.8	—
Indo-Pacific black marlin	*Makaira indica*	3	3	238–240	2	100	—
Indo-Pacific blue marlin	*Makaira mazara*	2	0	—	—	0	—
Pelagic stingray	*Pteroplatytrygon violacea*	12	5	—	2	41.2	—

0% to 40% on the hooks increased CPUE, but that the effect was not increased beyond this threshold. In contrast, blue shark had an increase in CPUE when the proportion of lightsticks was increased. Beyond an interest in understanding the influence of lunar periodicity and operational factors on the behavior of large pelagic fishes, these potential mechanisms are also of interest to fishermen, and our results also have implications for current and future fishing practices.

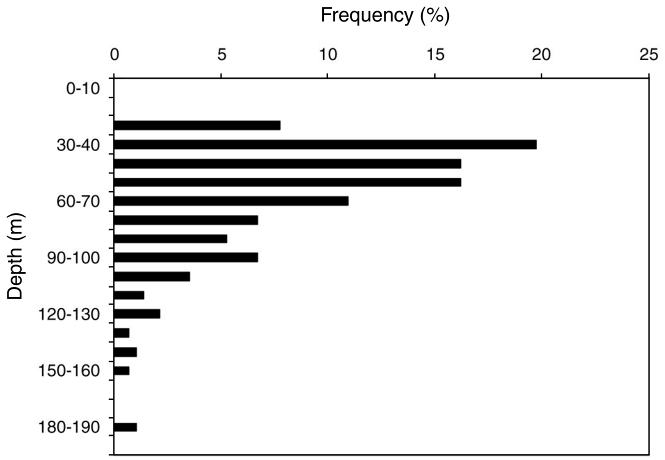

Figure 7

Pooled data from the time-depth recorders located on the mainline in the middle position between two consecutive floats during experimental sets (n=284) in the domestic Réunion Island longline fishery.

Adjustments of fishing strategy and future research needs

This study may help fishermen to modify fishing operations and select a fishing strategy to increase economic benefits and reduce the impact of bycatch mortality. Captains would be able to switch fishing practices to target one species or another according to lunar phase. Moreover, shifting from expensive squid to cheaper mackerel bait to catch albacore could reduce the operational costs during trips in October and November when albacore CPUE is seasonally highest.

We suggest that shortening the soak time during the fishing operation should be beneficial because the major portion of the catch occurred in the first few hours of the operation (presumably bait decreases in quality with time and there is an increase in bait loss) (Lokkeborg and Pina, 1997). Hook-timers and direct observations indicated that swordfish could escape for several hours after capture. Many triggered hook-timers were retrieved without a fish (1301 cases) and they may have been triggered for a variety of reasons, such as being triggered during deployment or retrieval operations, being activated by squids, or may have been triggered by the escape of fishes or turtles. Although we cannot assume that high escape rates have occurred, we had the opportunity to film a swordfish escaping during the hauling of the gear. It succeeded in unhooking itself at the surface but sank immediately from exhaustion. Therefore, even if the fate of the escaped animal was unknown, we assumed that a large proportion of swordfish might die from ingestion of the J hooks. In addition, long soaking periods in warm temperatures increase the degradation of flesh, reducing the market price of the fish. Shortening the soaking time could reduce the chance of depredation by large marine mammals (e.g., false killer whale [*Pseudorca crassidens*], shortfin pilot whale [*Globicephala macrorhyncus*]) and sharks on longline-caught fish. In the United States, limits on the length of a pelagic longline set have been proposed as a management measure to reduce bycatch (Kerstetter, 2008). It has been demonstrated that such a restriction would reduce the interaction rate of longlines with marine mammals in the Mid-Atlantic Bight by approximately 26%.[1]

The survival rates for blue shark and oceanic whitetip shark were estimated to be 49% and 41%, respectively. The survival rate of blue shark at haulback after a soak during the night was lower than that during day longline sets: 100% (Boggs, 1992), 80–90% (Campana et al., 2005), 69% (Diaz and Serafy, 2005), and 87% (Francis et al., 2001). Differences in survival rates among studies may result from hook types, leader material (monofilament or wire), and handling procedures, although survival rates between day and night longlining should be further investigated. Nevertheless, reducing the soaking period would increase the number of sharks released alive. The release of live bycaught sharks (Moyes et al., 2006) and billfish (Kerstetter and Graves, 2006, 2008) is by far the best management measure to reduce longline fishing mortality of these species.

From a cost benefit perspective, fishermen believe that chemical lightsticks improve fishing performance but they limit the number deployed because of the price. However, our data strongly indicate that the use of lightsticks did not increase swordfish catch by very much. Lightsticks are suspected to attract sea turtles to the vicinity of longlines (Wang et al., 2007) and thus may increase their incidental catch; however, lightsticks have a limited lifespan and are not reusable and thus are an environmental concern. Thousands of spent lightsticks are discarded at sea and constitute a potential toxicant to marine flora and fauna. In the case of Réunion Island, local fishermen were keen to retain used chemical lightsticks onboard, store them during the fishing trip, and offload them when returning to port after a significant awareness campaign about the negative environmental impact of lightsticks. In light of our results and for ecological concerns (Ivar do Sul et al., 2009; Pinho et al., 2009), the use of chemical lightsticks should be reconsidered. Recently, the working group of the General Fisheries Commission for the Mediterranean (GFCM) has proposed a ban on chemical lightsticks and any light source in the pelagic longline fishery in the Mediterranean Sea.[2]

Complementary three-dimensional acoustic telemetry experiments are needed to better understand the movements of swordfish and to test the hypothesis that tidal and oceanic currents may influence their foraging behavior and fishing operations associated with their foraging behavior. We also recommend additional studies to understand the interaction of lunar luminescence and swordfish size because of concerns for the sustainability of swordfish stocks and for the protection of certain age classes (Poisson and Fauvel, 2009).

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