291

RESEARCH COMMUNICATIONS RESEARCH COMMUNICATIONS.

Looking behind the curtain: quantifying massive shark mortality in fish aggregating devices

John David Filmalter^{1,2,3*}, Manuela Capello⁴, Jean-Louis Deneubourg⁴, Paul Denfer Cowley², and Laurent Dagorn¹

Increasing catch rates are considered the main impact of dynamic fisheries practices on marine ecosystems, but other effects can be equally important and are often ignored. Here we quantify a major, previously unknown source of shark mortality: entanglement in drifting fish aggregating devices, now widely used in the global tropical tuna purse-seine fishery. Using satellite tagging and underwater observational data, we developed two novel, independent, and complementary approaches, which quantify and highlight the scale of this problem. Entanglement mortality of silky sharks (*Carcharhinus falciformis*) in the Indian Ocean was 5–10 times that of the known bycatch of this imperiled species from the region's purse-seine fleet. More importantly, these estimates from a single ocean (480 000–960 000 silky sharks) mirror those from all world fisheries combined (400 000–2 million silky sharks), a situation that clearly requires immediate management intervention and extensive monitoring.

Front Ecol Environ 2013; 11(6): 291–296, doi:10.1890/130045 (published online 27 Jun 2013)

Tuman-induced impacts on marine populations are Human-induced impacts on manner reresources, which is generally regarded as the largest direct anthropogenic effect on marine ecosystems. However, other more complex issues - including global warming (Schmittner 2005; Cheung et al. 2010), ocean acidification (Caldeira and Wickett 2003), trophic cascades due to the removal of entire ecosystem tiers (Jackson et al. 2001; Myers et al. 2007), marine pollution (Halpern et al. 2008), and technological shifts in fishing practices - may ultimately have impacts equaling or even surpassing those caused by ongoing harvestrelated exploitation; impacts associated with these processes are harder to quantify because they are not easily observable or go unobserved at short timescales. The current methodology used to assess marine population health often excludes such processes and instead relies almost entirely on a single parameter, the amount of biomass extracted, which has been observed and quantified for decades. Although the impacts of these processes are often complex and difficult to measure and remedy, their mitigation in some cases may be relatively simple. Here we quantify and provide solutions for a previously unknown impact of a technological shift in the global tuna (Scombridae) purse-seine fishery, representing an extensive new source of mortality for a pelagic shark species already designated as Near

¹Institut de Recherche pour le Développement, Sète, France ^{*}(johndavid.filmalter@ird.fr); ²South African Institute for Aquatic Biodiversity, Grahamstown, South Africa; ³Department of Ichthyology and Fisheries Science, Rhodes University, Grahamstown, South Africa; ⁴Service d'Ecologie Sociale, Université Libre de Bruxelles, Brussels, Belgium Threatened by the International Union for Conservation of Nature (Bonfil *et al.* 2009).

During the past 20 years, the tropical tuna purse-seine fishery, operating throughout oceans worldwide, has changed its typical fishing practice. Traditionally, tuna schools were caught when feeding at the surface or when associated with marine mammals (Scott et al. 2012) or drifting logs (Freon and Dagorn 2000). More recently, the use of artificial fish aggregating devices (FADs) has become widespread. FADs work by taking advantage of the propensity of tropical tunas to aggregate around floating objects (Parrish and Edelstein-Keshet 1999). Once deployed, a FAD is left to drift freely in the open ocean for several months, with its spatial location monitored remotely via a satellite-tracked buoy (Dagorn et al. 2012). The FADs are then revisited by fishing vessels and the aggregated tuna and associated bycatch species captured. This fishery enhancement tool now accounts for >40% of all of the world's annual tropical tuna catch (4 million tons; Miyake et al. 2010). These FADs usually consist of bamboo poles bound with old netting, which extends to varying depths below the water's surface. The subsurface structure of a FAD is believed to aid in the attraction of small fish and serves to increase drag, ensuring ocean currents rather than wind drive the direction of its drift. These functions are important to fishers, who consider them essential for the formation of tuna aggregations. This netting can entangle marine animals, but because of the difficulty involved in observing such mortality events, they have largely been ignored by marine scientists and resource managers. The popularity of FADs in tuna purse-seine fleets has led to global concerns over the increased capture of undesirable sized tunas and bycatch, which include vulnerable pelagic

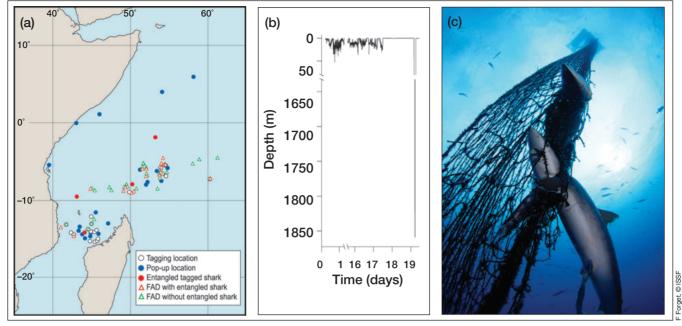


Figure 1. (a) Study area showing PSAT tagging and pop-up locations as well as locations of underwater observations at drifting FADs in the western Indian Ocean. (b) Typical depth profile received from a PSAT on a silky shark that became entangled. (c) Juvenile silky sharks entangled in the subsurface structure of a drifting FAD.

shark species (Gilman 2011). The silky shark (Carcharhinus falciformis) constitutes up to 90% of the elasmobranch bycatch in this fishery (Gilman 2011). Localized depletion is a concern in many parts of this shark's circumglobal distribution (Bonfil 2008; Anderson and Jauharee 2009; Bonfil et al. 2009) because it is also captured in greater numbers by other fishing gears including longlines and gillnets (Bonfil 2008; Gilman 2011; Hall et al. 2012). Juveniles of this species regularly associate with drifting objects (Anderson and Jauharee 2009; Filmalter et al. 2011), accounting for their prevalence in FAD fishing sets. This behavior also results in their entanglement in the netting of the FADs themselves, a previously unknown source of mortality. The now widespread use of FADs could pose a major risk to silky shark populations and requires quantification. Currently no methods exist for investigating "ghost fishing" on the high seas. This work aims to provide the first quantitative results for evaluating the scale of this problem in the Indian Ocean, as well as outlining new experimental and analytical approaches that can be used for future assessments in other fisheries or oceans.

Materials and methods

Satellite tagging: estimating the average time before entanglement

A total of 43 silky sharks were captured and fitted with pop-up satellite archival tags (PSATs; product name "MiniPAT", Wildlife Computers, Redmond, WA) during six cruises conducted between 2010 and 2012 offshore of the Republic of Seychelles and in the northern Mozambique Channel (Figure 1a). Sharks were caught either by handline from research vessels (n = 13) or during purse-seine operations on commercial vessels (n =30). Those caught from purse-seine vessels were tagged to investigate their post-release survival. Tags were attached either to a single threaded nylon rod secured through the first dorsal fin (n = 11) or by a nylon anchor, to which the tag was tethered, which was inserted into the dorsal musculature at the base of the first dorsal fin (n = 32). For the analysis presented here, only sharks that did not display direct post-release mortality (ie immediately sinking to a depth of >1600 m after release) were included, which led to a total of 29 individuals (WebTable 1).

Analysis of the detailed time-series depth profiles received from the tags clearly indicated that some of the individuals had succumbed as a result of FAD entanglement (WebPanel 1). The data series revealed an abrupt cessation of vertical movements followed by a constant depth reading close to the surface for extended periods (0.34–2.40 days; WebTable 2). After death by entanglement, the tagged sharks then sank to a depth >1600 m, causing the tag to automatically release and float to the surface (Figure 1b).

Using the data received from PSATs, we were able to estimate the daily probability of a silky shark becoming entangled in a FAD. Achieving this required that we consider the observation duration of all tagged sharks, as this differed between individuals owing to the premature shedding of many tags. Considering t = 0 as the tagging time, we denote the total number of sharks that are still observed at time t as $N_{tot}(t)$. Because $N_{tot}(t)$ varies in time due either to tag shedding or to

entanglement events, we can express its temporal variation through:

$$\frac{dN_{tot}(t)}{dt} = -\alpha_e N_{tot}(t) - \alpha_s N_{tot}(t)$$
 (Equation 1)

where α_e denotes the probability of entanglement and α_s the probability of tag shedding; both probabilities are assumed to be time-independent. From Equation 1, we can express the number of sharks that are still observed at time *t* as:

$$N_{tot}(t) = N_{tot}(0) \exp[-(\alpha_e + \alpha_s)t]$$
 (Equation 2)

where $N_{tot}(0)$ is the total number of sharks released after tagging. The total number of entangled sharks at time *t*, denoted by $N_e(t)$, then reads:

$$N_{\rm e}(t) = \int_0^t \alpha_{\rm e} N_{\rm tot}(t) dt = \alpha_{\rm e} N_{\rm tot}(0) \frac{\{1 - \exp[-(\alpha_{\rm e} + \alpha_{\rm s})t]\}}{\alpha_{\rm e} + \alpha_{\rm s}}$$
(Equation 3)

that, for large observation times t_{∞} , leads to the following expression for α_e :

$$\alpha_{e} = \frac{N_{e}(t_{\infty})}{N_{tot}(0)} (\alpha_{e} + \alpha_{s})$$
 (Equation 4)

The value of the exponent ($\alpha_e + \alpha_s$) was obtained through a survival curve analysis of the number of sharks still observed at time *t* (Equation 2), fitting the cumulative distribution of $N_{tot}(t)$ with an exponential model. From Equation 4, the average time required for a silky shark swimming in an environment with FADs to become entangled was estimated as $1/\alpha_e$.

Underwater observations: estimating the daily probability of a FAD entangling a shark

In addition to the tagging data, underwater observations were conducted between 2010 and 2012 by divers at 51 FADs with subsurface netting (Figure 1, a and c). During these observations, the presence and number of entangled sharks were noted (WebTable 3). Using a bootstrap resampling method (Efron and Tibshirani 1993) run with 1000 iterations, we then estimated the average and standard error of the number of FADs with zero, one, and two entangled silky sharks. From this dataset, we could estimate the daily probability of a FAD entangling a shark, taking into account both the possibility that a single FAD could entangle multiple sharks and that sharks could remain entangled for several days. Given X_0 as the number of FADs with zero entangled sharks and X_i as the number of FADs with a non-zero number of entangled sharks *j*, we expressed their time dependence through the following system of differential equations:

$$\begin{aligned} \frac{dX_0}{dt} &= -\mu X_0 + \theta X_1 \\ \frac{dX_j}{dt} &= -\theta j X_j - \mu X_j + \mu X_{(j-1)} + \theta (j+1) X_{(j+1)} & \text{for } j \neq 0 \end{aligned}$$
(Equation 5)

where μ is the probability of a FAD entangling a silky shark and θ is the probability of the entangled shark dropping out of the net. To adopt the most parsimonious model, we considered that the parameters μ and θ were constant for all FADs. For any value of entangled sharks per FAD *j*, Equation 5 leads to the stationary solutions:

$$X_{j} = \frac{1}{j!} \left(\frac{\mu}{\theta}\right)^{j} X_{0}$$
 (Equation 6)

Considering that the sum of the number of FADs with *j* entangled sharks must equal the total number of observed FADs (denoted as N_{FAD}), the estimated daily probability of a FAD entangling a shark μ is expressed as:

$$\mu = -\theta \ln \left(\frac{X_0}{N_{FAD}}\right)$$
 (Equation 7)

The factor θ was obtained from a survival curve analysis of the observed time individuals spent entangled (dead) in the net before sinking, from the PSAT dataset (WebFigure 1; WebTable 2). For this purpose, we adopted the most parsimonious model for survival events – that is, a single exponential model of the form $f(t) = \exp(-\theta t)$ – and fitted this to the observed entanglement duration data.

Several factors may influence the time an entangled shark will remain in the netting of a FAD. Many species of fish - including the oceanic triggerfish (Canthidermis maculata) and rainbow runner (Elagatis bipinnulata) – commonly aggregate around FADs in the Indian Ocean. When a shark becomes entangled, these fish often feed on its carcass. Some entangled sharks were also observed with large portions of musculature removed, very likely by other, larger sharks. As the carcass is broken up due to this predation, it falls from the net and sinks. In addition, the manner in which sharks become entangled can vary greatly, from being strongly meshed behind the gills and around the head to simply being wrapped up with the net hooked on the jaw. These and other factors, such as the prevailing state of the sea, which will influence the jerking motion of the net, interact to determine how long the shark's carcass will remain in the net.

Results

Four of the 29 sharks tagged became entangled after 4–94 days at liberty (Table 1). The exponential model fitted to the tagging observation duration data produced an exponent of 0.024 (Figure 2). Following Equation 1, the average time required for an individual silky shark swimming in an environment with FADs to become entangled was estimated as 300 ± 45 days. From growth models

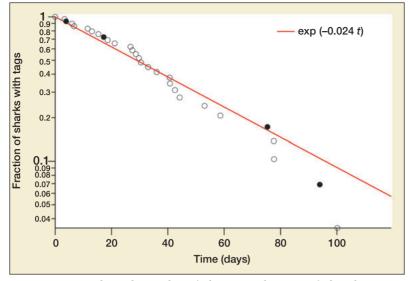


Figure 2. Semi-logarithmic plot of the survival curve of the observation durations for silky sharks tagged with PSATs fitted with an exponential function of the form $f(t) = exp[-(\alpha_e + \alpha_s)t]$. Solid black circles represent entangled individuals; open circles represent individuals that avoided entanglement.

(Joung *et al.* 2008) and catch size frequencies (Amandé *et al.* 2010), we know that silky sharks found around FADs are generally in their first 3 years of life. Integrating the estimated average entanglement time of 300 days into an exponential survival model, we found that the entanglement mortality is 71% \pm 4% after one year. Following this rate, the number of sharks avoiding entanglement after 3 years is only 2.6% \pm 0.4% (Figure 3a).

Results from the underwater observation dataset revealed that 35% of FADs surveyed had at least one entangled silky shark (Table 2). The estimated value of θ was $\theta = 0.85 \pm 0.1$ days⁻¹ (see WebFigure 1), which led to an average time spent entangled in the net of approximately 1.2 \pm 0.2 days. Integrating this result into Equation 7, we estimated the daily probability of a FAD entangling a shark as $\mu = 0.35 \pm 0.08$.

To test the validity of our model (Equation 5), we performed a chi-square test of homogeneity between the theoretical Poisson distribution (Equation 6) and the experimental distribution of FADs with zero, one, and two entangled sharks (Table 2). The test indicates that we can accept the null hypothesis of homogeneity between the two distributions for values of μ between 0.25 (4 days) and 0.6 (2 days), which validates our model and results (see WebFigure 2).

To extrapolate our predictions to the ocean basin, we

Table 1. Time at liberty before entanglement for fourindividual silky sharks tagged with PSATs			
Shark ID	Time at liberty (days)		
4	94		
8	75		
19	17		
13	4		

www.frontiersinecology.org

considered different numbers of FADs active per day in the Indian Ocean (WebPanel 2). Assuming the presence of between 3750 and 7500 active FADs (Figure 3b), estimates of between 480 000 \pm 110 000 and 960 000 \pm 220 000 silky sharks are killed per year, respectively.

Discussion

The high frequency of entanglement events that we observed provides preliminary evidence that the impact of FADs is severe. Although uncertainty is inherent and unavoidable in this type of study (Piatt and Ford 1996), this first quantitative estimate serves to highlight both the extent of this issue and the need for immediate attention. Our study is based on two approaches that are not typically used concomitantly: behavioral information (obtained through satellite tagging) and count statistics (generally used in population analyses, but novel here because they incorporate underwater observations from the pelagic realm). The fact that these two independent experimental protocols both signal high rates of entanglement reinforces our predictions.

The mortality rates reported here are concerning, and lead directly to questions regarding their effects on populations. Owing to the absence of catch data from other types of fishing gear believed to substantially impact silky sharks in the Indian Ocean (gillnets and longlines), any attempt at assessing their population status in this region is impossible (Bonfil 2008). However, the little information available suggests strong declines in recent decades (Anderson and Jauharee 2009). The fact that juvenile silky sharks are still regularly encountered at FADs suggests that either a portion of the population may not be exposed to high FAD densities or the population effect of entanglement is delayed. Addressing the first hypothesis requires information on the spatial density distribution of juvenile silky sharks as well as FADs. However, these parameters are still unknown for the Indian Ocean. As for the second hypothesis, a delay in the population effect could be the result of several interacting factors. First, the individuals affected by entanglement are typically within the first 3 years of age. Second, silky sharks mature after approximately 10 years (Joung et al. 2008), and females generally produce between six to 12 offspring every 2 years (Bonfil 2008). Third, the use of FADs has recently increased greatly. As such, severe population impacts may only be observed in years to come.

To contextualize our results in relation to the observed bycatch mortality of silky sharks from the tuna purse-seine fishery in the Indian Ocean, we used data reported in Dagorn *et al.* (2012) on the amount of silky sharks (tons) caught per 1000 tons of tuna (WebTable 4). We then converted this to the number of individuals using the weight at 110 cm fork length, the peak of the observed bycatch



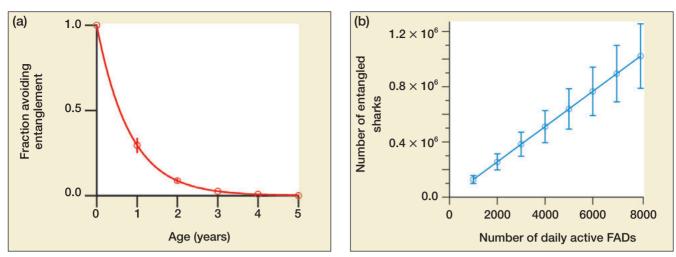


Figure 3. (a) Predicted survival curve of juvenile silky sharks due to entanglement, using an average time before entanglement of 300 days. The proportion of sharks surviving is 29% after one year, 9% after 2 years, and 3% after 3 years. (b) Estimated annual number of entangled sharks in the Indian Ocean as a function of the number of FADs active per day, from the estimated daily probability of a FAD entangling a shark of $\mu = 0.35$. Error bars in (a) and (b) indicate standard errors.

length frequency (Roman-Verdesoto and Orozco-Zoller 2005; Amandé et al. 2008), using published conversion factors (approximately 15 kg; Joung et al. 2008). This led to an average estimate of 82 000 silky sharks taken as bycatch in the Indian Ocean purse-seine fishery each year, an order of magnitude less than the mortality estimates presented here. Furthermore, following the same method, the global purseseine fishery catches an average of 158 000 silky sharks annually (Dagorn et al. 2012), which is still inferior to our lower estimate from the Indian Ocean. Our estimates are more comparable with the estimate of silky shark bycatch from longline vessels in the Central and South Pacific more than 20 years ago (900 000 individuals; Bonfil 1994) or the range of a more recent estimate from all of the world's fisheries combined, obtained from the shark fin trade in Southeast Asia (Figure 4; Clarke et al. 2006). Comparing our results with the situations in other oceans is currently impossible, because no similar data exist. Furthermore, we argue that extrapolation using regional FAD deployment figures alone should be avoided, given that entanglement probability is likely to vary between oceans due to both FAD design and silky shark abundance.

We recognize that the sample sizes used in this study are limited and that increasing sample sizes would improve the accuracy of our extrapolations. However, while improving data collection through widespread monitoring is impera-

Table 2. Number and frequency of FADs (with a net)
found with 0, 1, and 2 entangled sharks from under-
water observations

Number of entangled sharks per FAD	Number of observations (± SE)	Frequency (± SE)
0	33 (± 3.5)	65% (± 7%)
1	14 (± 3.1)	27% (± 6%)
2	4 (± 2.0)	8% (± 4%)
Notes: SE = standard error.		

tive, we argue that priority should be given to solving this issue. Despite these small sample sizes, both independent datasets suggest that FAD entanglement poses an immense threat to silky shark populations. Yet simple, cost-effective solutions exist that would promote the conservation of this species. Redesigning FADs by excluding meshed materials would eliminate this problem while sustaining the production of the fishery. Although these subsurface structures are of importance, the use of netting is not. Alternative materials that are biodegradable and provide zero chance of entanglement, such as sisal ropes, can offer effective substitutes.

Although the findings of this study reflect the impacts of a technological change on a single species of shark, the problem identified here is of wider importance. Fisheries managers require more adaptive approaches. While efforts are currently underway to improve the monitoring of catches and bycatch, we have shown that this information is not always adequate for detecting all impacts of changing fishery practices. As marine resources become scarcer, the technologies used to maintain efficient economic extraction rates will continue to develop. It is the responsibility of scientists and managers to identify such changes, along with all of their possible impacts, as and when they occur. FADs have been used with increasing frequency worldwide for the past 20 to 30 years, but it is only now that the unexpected impact on silky shark populations in the Indian Ocean has been detected. Clearly, such retrospective approaches will not lead to long-term sustainability of fisheries. Anticipation is essential to mitigating negative human-induced impacts on ecosystems and as such should be a cornerstone of resource management in the future.

Acknowledgements

We thank F Poisson, A Vernet, and F Forget for assistance with fieldwork. This research was financially supported by: the commission of the European communities, FP 7,



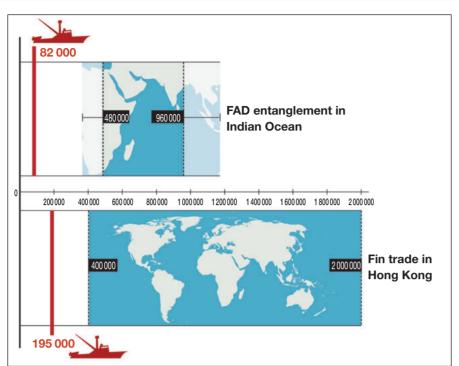


Figure 4. Estimated range of silky shark mortality due to FAD entanglement from the Indian Ocean (top) as compared with estimated silky shark mortality from all world fisheries from the shark fin trade in Hong Kong (bottom). Red lines indicate annual incidental capture in purse-seine fisheries at each scale.

"Theme 2–Food, agriculture, fisheries and biotechnology", through the research project MADE, contract No 210496; the Bycatch mitigation project of the International Seafood Sustainability Foundation; the ORTHONGEL-IRD project on bycatch mitigation; the Marie Curie IEF fellowship, project QUAESITUM, FP7 PEOPLE, contract No 299519; and the Belgium National Science Foundation (FNRS). This work does not necessarily reflect the commission's views and in no way anticipates its future policy in this area.

References

- Amandé MJ, Ariz J, Chassot E, et al. 2010. Bycatch of the European purse seine tuna fishery in the Atlantic Ocean for the 2003–2007 period. Aquat Living Resour 23: 353–62.
- Amandé MJ, Chassot E, Chavance P, et al. 2008. Silky shark (Carcharhinus falciformis) bycatch in the French tuna purseseine fishery of the Indian Ocean. Victoria, Seychelles: Indian Ocean Tuna Commission, IOTC WPEB – 2008/016.
- Anderson RC and Jauharee R. 2009. Opinions count: declines in abundance of silky sharks in the central Indian Ocean reported by Maldivian fishermen. Victoria, Seychelles: Indian Ocean Tuna Commission, IOTC-2009-WPEB-08.
- Bonfil R. 1994. Overview of world elasmobranch fisheries. Rome, Italy: FAO.
- Bonfil R. 2008. The biology and ecology of the silky shark, *Carcharhinus falciformis*. In: Camhi MD, Pikitch EK, and Babcock EA (Eds). Sharks of the open ocean: biology, fisheries and conservation. Oxford, UK: Oxford Blackwell Publishing Ltd.
- Bonfil R, Amorim A, Anderson C, et al. 2009. Carcharhinus falciformis. In: International Union for Conservation of Nature (IUCN) 2012: IUCN red list of threatened species. Version 2012.2. www.iucnredlist.org/details/39370/0. Viewed 2 May 2013.
- Caldeira K and Wickett ME. 2003. Anthropogenic carbon and ocean pH. Nature **425**: 365.

- Cheung WWL, Lam VWY, Sarmiento JL, et al. 2010. Large-scale redistribution of maximum fisheries catch potential in the global ocean under climate change. *Glob Chang Biol* **16**: 24–35.
- Clarke SC, McAllister MK, Milner-Gulland EJ, et al. 2006. Global estimates of shark catches using trade records from commercial markets. Ecol Lett 9: 1115–26.
- Dagorn L, Holland KN, Restrepo V, *et al.* 2012. Is it good or bad to fish with FADs? What are the real impacts of the use of drifting FADs on pelagic marine ecosystems? *Fish Fish*; doi:10.1111/j.1467-2979.2012.00478.x.
- Efron B and Tibshirani R. 1993. An introduction to the bootstrap. New York, NY: Chapman and Hall.
- Filmalter JD, Dagorn L, Cowley PD, *et al.* 2011. First descriptions of the behavior of silky sharks, *Carcharhinus falciformis*, around drifting fish aggregating devices in the Indian Ocean. *Bull Mar Sci* 87: 325–37.
- Freon P and Dagorn L. 2000. Review of fish associative behaviour: toward a generalisation of the meeting point hypothesis. *Rev Fish Biol Fish* **10**: 183–207.
- Gilman EL. 2011. Bycatch governance and best practice mitigation technology in global tuna fisheries. *Mar Policy* **35**: 590–609.
- Hall NG, Bartron C, White WT, *et al.* 2012. Biology of the silky shark *Carcharhinus falciformis* (Carcharhinidae) in the eastern Indian Ocean, including an approach to estimating age when timing of parturition is not well defined. *J Fish Biol* **80**: 1320–41.
- Halpern BS, Walbridge S, Selkoe KA, *et al.* 2008. A global map of human impact on marine ecosystems. *Science* **319**: 948–52.
- Jackson JBC, Kirby MX, Berger WH, *et al.* 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**: 629–38.
- Joung S-J, Chen C-T, Lee H-H, et al. 2008. Age, growth, and reproduction of silky sharks, *Carcharhinus falciformis*, in northeastern Taiwan waters. Fish Res 90: 78–85.
- Miyake MP, Guillotreau P, Sun C-H, *et al.* 2010. Recent developments in tuna industry: stocks, fisheries, management, processing, trade and markets. Rome, Italy: FAO.
- Myers RA, Baum JK, Shepherd TD, *et al.* 2007. Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* **315**: 1846–50.
- Parrish JK and Edelstein-Keshet L. 1999. Complexity, pattern, and evolutionary trade-offs in animal aggregation. *Science* **284**: 99–101.
- Piatt JF and Ford RG. 1996. How many seabirds were killed by the *Exxon Valdez* oil spill? *Am Fish Soc Symp* **18**: 712–19.
- Roman-Verdesoto M and Orozco-Zoller M. 2005. Bycatch of sharks in the tuna purse-seine fishery of the eastern Pacific Ocean reported by observers on the Inter-American Tropical Tuna Commission, 1993–2004. La Jolla, CA: Inter-American Tropical Tuna Commission.
- Schmittner A. 2005. Decline of the marine ecosystem caused by a reduction in the Atlantic overturning circulation. *Nature* **434**: 628–33.
- Scott MD, Chivers SJ, Olson RJ, et al. 2012. Pelagic predator associations: tuna and dolphins in the eastern tropical Pacific Ocean. Mar Ecol-Prog Ser 458: 283–302.

WebPanel 1.

Determining entanglement events and longevity

To verify that the data from the tags represented an entanglement event and not the behavior of the silky sharks (Carcharhinus falciformis), we developed a method based on the vertical behavior displayed by each individual throughout tag deployment. In addition to sharks outfitted with pop-up satellite archival tags (PSATs) becoming entangled, one C falciformis (77 cm total length) tagged with a pressure-sensitive acoustic tag (Vemco, Halifax, Canada), which had been surgically implanted inside the shark's peritoneal cavity, also became entangled. The time-series data from this tag were recorded and transmitted via a satellite-linked acoustic receiver (VR4-Global, Vemco), which was attached to the drifting fish aggregating device (FAD) where the shark had been tagged 5.42 days before. The data from this tag were included in the estimation of entanglement longevity. Here we define the time t_a as the point at which the shark became entangled and the time t_s as the point at which the shark sank from the net, with the tag still attached (WebFigure 3a). We considered the time interval (t_s-t_e) as the "entanglement longevity".

To distinguish the entanglement event from other periods of reduced vertical movements and to establish the temporal boundaries t_e and t_s of the time spent in the net, we developed the following approach. Time bins of 30 minutes were created, and average swimming depth D_j and its associated variance σ^2_{Dj} were calculated. We then identified periods of low vertical movement (LVM) as time windows where the shark's swimming behavior was characterized by a constant depth and very small vertical displacement within the temporal bin, based on two criteria:

- I. The variance of the depth σ^2_{Dj} of each bin constituting the LVM time window was smaller than 1 m.
- 2. For each bin *j* constituting the LVM time window, the consecutive bin *j*+1 also constituted the same LVM time window if the relative difference among their depth was smaller than 2 m $(|D_i D_i + 1| \le 2m)$.

These criteria were chosen according to the precision of the depth sensor of the tag (0.5 m). In this way, we identified several LVM time windows in the tagged sharks' behavior. We calculated the distribution, average value, and standard deviation of these LVM time windows, apart from the last one recorded before sinking, which was a candidate for an entanglement event. If the tagged shark was not observed sinking from the net (n = 1), we considered the entanglement longevity to be the last recorded period at a constant depth, which was not at the surface (>3 m). WebTable 2 shows the estimated entanglement times. The average LVM time window, other than the entanglement times, calculated for the entangled sharks corresponded to 0.64 ± 0.61 hours. The distribution of LVM time windows was highly skewed toward very short times \leq 30 min (WebFigure 4). Therefore, we could safely consider that the entanglement times in WebTable 2 corresponded to true entanglement events, since their durations were several standard deviations away from the average LVM window length.

Certainty of entanglement event

There are several possible interpretations of the vertical pattern observed in the PSAT datasets; however, none explain the pattern as well as that of an entanglement event.

Before considering the PSAT data, the interpretation of the acoustic tag data is equally as important and less complicated. This tag was internally implanted and is negatively buoyant. It can be detected only when within the range of the receiver, which is fixed to the FAD. The shark in question ceased all vertical displacement

after 5.42 days of "normal" behavior, and was continuously detected for 21.43 hours. The tag then sank out of the reception range. At this particular FAD, there were three other silky sharks tagged with acoustic tags, none of which displayed any change in behavior similar to the shark in question, suggesting that the receiver was functioning normally. Before these sharks were tagged, underwater observations were performed and the sharks and FAD-associated net were observed. Coupled with the regular observation of non-tagged sharks entangled in the nets of FADs, it is highly probable that this individual became entangled. After the 21.43 hours, either the shark fell from the net or the tag fell from its peritoneal cavity as other FAD-associated fish consumed its carcass.

The interpretation of PSAT data is more complicated given that these tags are buoyant and will float when deployment is terminated. There are several possible reasons for a tag deployment to be terminated, but again, none explain the observed vertical pattern as well as FAD entanglement.

First, if a tag becomes detached prematurely, either by the anchor working out of the musculature, or the tag being pulled off by another animal, it will float at the surface. There is no reason for it to suddenly sink after several hours or days of floating.

Second, if the tagged shark dies, it and the tag will sink, but then the observed constant depth prior to sinking is unlikely to occur. The analysis above clearly demonstrates that this constant depth is not part of the shark's natural behavior. If the shark was dying due to injuries from tagging or predation, it seems equally unlikely for it to be able to maintain a constant depth for such an extended period in the throes of death.

The shark possibly became entangled in something other than the netting of a FAD, such as a drifting gillnet; however, there are several lines of evidence to suggest that this is less likely. First, we have shown, through underwater observations, that these sharks *do* become entangled in FADs, irrespective of whether they were tagged. Second, as these sharks associate with drifting objects for extended periods (at least several days at a time), they are constantly exposed to the possibility of entanglement. Finally, although poorly documented, the use of pelagic gillnets is known to be far less common in the equatorial western Indian Ocean, where the suspected entanglements occurred, than in waters north of 10°N. Conversely, the distribution of FADs encompasses the entire area where sharks were tagged and where suspected entanglements occurred.

For all of these reasons, the possibility that something other than entanglement led to the consistent patterns observed in the four PSAT data series seems highly unlikely.

Species concerned

Only two species of elasmobranch regularly associate with drifting objects, the silky shark and the oceanic whitetip shark (*Carcharhinus longimanus*). Silky sharks are far more common, representing more than 90% of the elasmobranch catch in FAD sets. It is certainly the associative behavior that leads to the entanglement of silky sharks. Furthermore, because those that associate are juveniles, they match the mesh size of the netting that is regularly used in FAD construction. As such, the potential for the net to act as a gillnet is almost optimized for this small size of shark. The juveniles of other common pelagic shark species, such as the blue shark (*Prionace glauca*), typically occur in more temperate waters beyond the bounds of the FAD fishing activity. The possibility that another species of shark can become entangled in a FAD cannot be denied but it is certainly far less likely.

WebPanel 2. Estimating total FAD numbers in the Indian Ocean

Quantification of the number of *Carcharhinus falciformis* killed through entanglement annually in the Indian Ocean required the estimation of the number of FADs active on a daily basis. The fishery consists almost entirely of Spanish, Seychelles, and French flagged vessels. As information on FAD deployment is not readily available, we used fleet-specific data and trends. The Spanish fleet (13 vessels) reported the deployment of 3692 FADs with nets in 2010 to the Indian Ocean Tuna Commission (data from IOTC). Additionally, eight vessels, with Spanish skippers but flagged in Seychelles, did not report these data but were assumed to operate in the same manner, and as such, deploy 2272 FADs annually. The French fleet (13 vessels) has a self-imposed limit of 200 tracking buoys per vessel per year and consequently deploys a maximum of 2600. We know that 58% of these buoys are deployed on FADs (Moreno *et al.* 2007a), leading to 1508 FADs annually. Adding these three figures gives an approximate estimate of 7500 FADs deployed annually that could entangle sharks. This estimate is probably only accurate in terms of the order of magnitude, due to poor data reporting since the emergence of the FAD fishery.

As FADs undergo cycles of serial ownership, their absolute history and life span is masked. Some evidence suggests that FAD lifetime may be as long as one year (Moreno et al. 2007a), whereas a more conservative estimate suggests 6 months. As such, we obtained estimates of 3750 and 7500 FADs active on a daily basis. This compares well with the estimated 2500 FADs active daily, obtained from interviews with skippers in 2004 and 2005 (Moreno et al. 2007b).

ldentity code	Tagging date	Total length (cm)	Sex	Observation time (days)
I	13/03/2010	88	F	18
2	15/03/2010	109	М	100
3	15/04/2011	91	М	26
4	20/04/2011	98.5	М	94 *
5	20/04/2011	103	F	11
6	18/06/2011	98	F	6
7	20/06/2011	93	М	32
8	20/06/2011	102	М	75*
9	13/04/2012	109	F	119†
10	13/04/2012	111.8	F	30†
11	14/04/2012	111.3	-	29†
12	14/04/2012	116	-	58†
13	14/04/2012	116	М	4*†
14	26/03/2011	137	F	2
15	27/03/2011	127	F	6
16	28/03/2011	140	М	27
17	28/03/2011	86	F	44
18	31/03/2011	100	F	15
19	01/04/2011	87	F	17*
20	01/04/2011	98	F	21
21	01/04/2011	87	М	36
22	02/04/2011	155	-	13
23	25/05/2011	122	F	53
24	25/05/2011	150	М	40
25	02/04/2012	104	М	28
26	02/04/2012	113.6	F	40
27	03/04/2012	132	М	77
28	03/04/2012	155	М	42
29	06/05/2012	104	-	77†

WebTable 1. Metadata of juvenile silky sharks (*Carcharhinus falciformis*) tagged with PSATs at drifting FADs in the Indian Ocean

Notes: Sharks 1–13 formed part of behavioral studies whereas sharks 14–29 were tagged to study post-release survival. Asterisks denote individuals that became entangled. Tags were programmed to release after 100 days except those marked with the single dagger, which were set for 150 days.

WebTable 2. Entanglement times estimated for four sharks outfitted with PSATs and one acoustically* tagged shark

ldentity code	Entanglement time (hours)
64*	21.43
4	7.92
8	54.42
19	37.83
13	25.17

WebTable 3. Data from underwater observations at FADs with nets

neto		
	Number of	Number of
FAD	sharks entangled	free sharks observed
1		0
2	2	0
3	0	2
4	0	6
5	0	0
6	0	0
7	I	0
8	1	25
9	1	15
10	0	10
11	0	10
12	I	10
13	2	4
14	0	3
15	I	2
16	0	2
17	2	1
18	0	5
19	0	I
20	0	3
21	l	5
22	0	0
23	0	3
24	l	0
25	0	7
26	0	0
27	0	0
28	0	0
29	I	0
30	0	0
31	0	0
32	0	0
33	I	0
34	0	0
35	0	0
36	0	0
37	0	3
38	0	0
39	I	3
40	0	I
41	0	0
42	I I	l
43 44	2	0 I
44 45	0	0
45 46	0	2
46 47	0	2
48	0	2
40 49	0	2
50	I	2
50	0	7
51	v	/

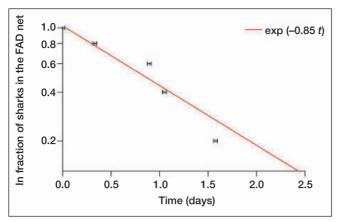
WebTable 4. Data used to estimate silky shark bycatch in number of individuals from each ocean area, taken from Dagorn *et al.* (2012)

	EPO	AO	10	WCPO	Total
Tons of sharks per 1000 t FAD tun	a 1.9	1.8	6	1.1	10.8
Landed BET (t)	70 000	15750	21 000	47 500	154250
Landed SKJ (t)	151680	80 900	151590	857 920	I 242 090
Landed YFT (t)	35 700	14040	55 590	178 560	283 890
Total tuna (t)	257 380	110690	228 80	I 083 980	I 680 230
Total sharks (t)	440.1198	179.3178	1232.172	1073.1402	2924.7498
Number of silky sharks	29341	955	82 45	71 543	194983
N . 500 D 10 0 10					

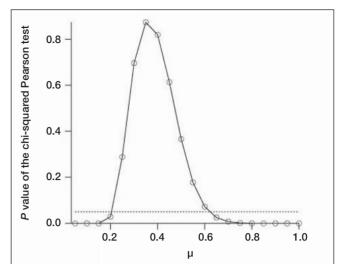
Notes: EPO = eastern Pacific Ocean, AO = Atlantic Ocean, IO = Indian Ocean, WCPO = western and central Pacific Ocean. Data are reported by species: BET = bigeye tuna (*Thunnus obesus*), SKJ = skipjack tuna (*Katsuwonus pelamis*), and YFT = yellowfin tuna (*Thunnus albacares*).

WebReferences

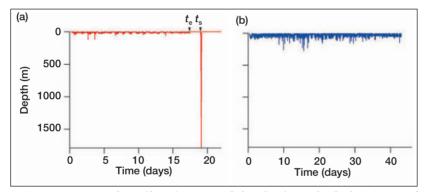
- Dagorn L, Holland KN, Restrepo V, *et al.* 2012. Is it good or bad to fish with FADs? What are the real impacts of the use of drifting FADs on pelagic marine ecosystems? *Fish Fish*; doi:10.1111/j.1467-2979.2012.00478.x.
- Moreno G, Dagorn L, Sancho G, *et al.* 2007a. Using local ecological knowledge (LEK) to provide insight on the tuna purse seine fleets of the Indian Ocean useful for management. *Aquat Living Resour* **20**: 367–76.
- Moreno G, Dagorn L, Sancho G, et al. 2007b. Fish behaviour from fishers' knowledge: the case study of tropical tuna around drifting fish aggregating devices (DFADs). Can J Fish Aquat Sci 64: 1517–28.



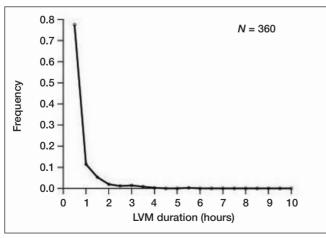
WebFigure 1. Survival curve of entanglement durations. Semilog plot of the survival curve of entanglement durations from juvenile silky sharks tagged with pressure-sensitive electronic tags fitted with an exponential function of the form $f(t) = exp(-\theta t)$.



WebFigure 2. Validating model predictions. P values of the comparison between underwater observation data of silky sharks entangled in FADs and the theoretical Poisson distribution calculated with different values of μ . The test of comparison was the chi-square test.



WebFigure 3. Depth profiles of an entangled and a free individual. (a) Typical depth profile of a tagged shark that became entangled during the monitoring period, from tagging to entanglement. Arrows labeled t_e and t_s indicate the entanglement time and sinking time, respectively. (b) Typical depth profile of a tagged shark that did not become entangled.



WebFigure 4. Distribution of LVM windows. Distribution of LVM times from the entangled sharks.