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Vulnerability of oceanic sharks as pelagic longline bycatch

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ABSTRACT

Bycatch (the unintentional catch of non-target species or sizes) is consistently ranked as one of the greatest threats to marine fish populations; yet species-specific rates of bycatch survival are rarely considered in risk assessments. Regulations often require that bycatch of threatened species be released; but, if animals are already dead, their release serves no conservation purpose. We examined the survival of 12 shark species caught as bycatch in the US Atlantic pelagic longline fishery. Shark survival was evaluated in relation to fishery target (swordfish versus tuna) and four operational, environmental, and biological variables to evaluate the underlying mechanisms affecting mortality. Survival estimates ranged from 33% (night shark) to 97% (tiger shark) with seven of the 12 species being significantly affected by at least one variable. We placed our survival results within a framework that assessed each species' relative vulnerability by integrating survival estimates with reproductive potential and found that the bigeye thresher, dusky, night, and scalloped hammerhead shark exhibited the highest vulnerabilities to bycatch. We suggest that considering ecological and biological traits of species shows promise for designing effective conservation measures, whereas techniques that reduce fisheries interactions in the first place may be the best strategy for highly vulnerable species.

1. Introduction

Overfishing represents the greatest threat to marine fish stocks globally (Hutchings and Reynolds, 2004; Jackson et al., 2001; Pauly et al., 2002) and substantial research has focused on better understanding the vulnerabilities and resilience of marine species to sustained fishing (Dulvy et al., 2008; Worm and Branch, 2012). Modeling and ranking the vulnerabilities of dissimilar species to fisheries capture can provide insight into how fishery-related stressors affect ecologically/biologically similar (or different) species as well as provide a mechanism for prioritizing species for conservation actions (Astles et al., 2006; Gallagher et al., 2012).

Elasmobranchs are particularly vulnerable to overfishing due to their relatively low reproductive output and low potential for population recovery compared to most teleosts (Myers and Worm, 2005; Stevens et al., 2000). Several elasmobranchs are experiencing drastic population declines across their range (e.g., Baum et al., 2003; Dulvy et al., 2008;

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Ferretti et al., 2010). While many shark species are targeted for the global shark fin trade or otherwise retained for consumption (Clarke et al., 2006; Worm et al., 2013), elasmobranchs are also unintentionally caught as bycatch in many fisheries, and this catch can often exceed that of the actual targeted species (Bonfil, 1994; Molina and Cooke, 2012). Bycatch is often (but not always) discarded regardless of their at-vessel status (live, injured or dead), and is poorly reported in some fishery records making it difficult to assess impacts (Barker and Schluessel, 2005; Bonfil, 1994). Additionally, management regulations often require that bycatch of threatened species be released to promote their conservation (Molina and Cooke, 2012); however, if fishes are dead upon gear retrieval then such practices can be futile for conservation efforts. However, understanding the at-vessel status of individuals caught as bycatch and modeling their survival in light of biological, environmental, and operational variables can provide insights into the underlying mechanisms driving mortality, thus informing which aspects of a fishery might be modified to mitigate lethal effects of capture on a species-specific basis (Serafy et al., 2012).

Longline fishing provides one of the largest sources of fisheries interactions with sharks, and it is well known that species with limited biological productivity are among the most vulnerable to many, if not all forms of fishing mortality, including bycatch (Cortés et al., 2010). Previous studies describing the observational at-vessel survival rates of certain shark species in both pelagic and bottom longline fisheries have documented a wide range of estimated survival rates among species (e.g. Beerkircher et al., 2002; Diaz and Serafy, 2005; Morgan and Burgess, 2007; Morgan and Carlson, 2010). This work has provided a strong foundation to begin asking additional questions about how bycatch affects the survival of shark species; specifically, assessing the potential influences of operational, environmental and biological variables of the fishery under investigation. For example, pelagic longline fisheries often switch between fishery targets (i.e., tuna versus swordfish), thereby altering environmental (time of day) and operational (fishing depth) aspects of the fishery. However, it is unclear if and how these operational differences affect the survival of sharks captured as bycatch. Thus, there is a need to model species-specific survival in light of fishery targets and other potentially significant variables which may affect survival.

To address these gaps, the present study provides an assessment of at-vessel hooking survival for 12 shark species encountered as bycatch in the US Atlantic pelagic tuna and swordfish longline fishery from 1995 to 2012. Study objectives were to: (1) determine the influence of fishery target (tuna or swordfish) as well as various operational (soak time and hook depth), environmental (sea surface temperature) and biological (animal length) variables on shark bycatch survival to evaluate the potential underlying mechanisms driving at-vessel mortality and; (2) determine and rank species-specific hooking survival rates (i.e., proportion alive upon gear retrieval) for the 12 focal shark species after adjusting for these variables. To generate an overall index of relative vulnerability to bycatch, we integrated our results into a framework that incorporated species-specific reproductive potential (age at maturity and fecundity). The novelty in our study resides in the ability to assess the influence of fishery-related variables on survival, as well as by controlling for these variables when generating new survival estimates from nearly two decades of bycatch data. Our findings are discussed in terms of each species' phylogeny, conservation status, reproductive output, physiology, and degree of specialization in selected functional and behavioral traits (Gallagher et al., 2014a).

2. Methods

2.1. Study and data location

The US pelagic longline fishery operates year-round throughout the western Atlantic Ocean and primarily targets swordfish (*Xiphius gladius*), yellowfin tuna (*Thunnus albacares*), and bigeye tuna (*Thunnus obesus*). In the present study, we used shark bycatch data derived from the tuna- and swordfish-directed pelagic longline fishery in the western Atlantic Ocean and Gulf of Mexico from 1995 to 2012. Set-specific data were provided by the US National Marine Fisheries Service (NMFS) Pelagic Observer Program (POP). The POP gathers detailed information on each longline set including: target species, time and location of deployment, hook type, number of hooks, number of light sticks, bait, soak duration, sea surface temperature, and estimated hook depth. Information is also collected on the details of catch, such as the identity (species and/or genus) of captured taxa, their numbers, their size (fork length, FL; visually estimated) and their status (live/dead/damaged) at boatside when the longline gear is retrieved. Sharks are classified as "dead" if they show no visible movement. If a shark is either dead or alive, but exhibits extensive injuries, the fish is classified as "damaged". Further details of observer protocols are available at http://www.sefsc.noaa.gov/fisheries/observers/forms.htm.

2.2. Species assessed

We focused our analyses on 12 shark species that are readily identifiable (with training) at the species level and commonly captured as bycatch with both tuna- and swordfish-directed pelagic longline gear in the Atlantic Ocean and/or Gulf of Mexico. These shark species included: bigeye thresher (*Alopias superciliosus*), blue (*Prionace glauca*), dusky (*Carcharhinus obscurus*), longfin mako (*Isurus paucus*), night (*Carcharhinus signatus*), oceanic whitetip (*Carcharhinus longimanus*), porbeagle (*Lamna nasus*), sandbar (*Carcharhinus plumbeus*), scalloped hammerhead (*Sphyrna lewini*), shortfin mako (*Isurus oxyrinchus*), silky (*Carcharhinus falciformis*), and tiger (*Galeocerdo cuvier*).

2.3. Analyses and survival estimates

To test the hypothesis of no influence of operational (target, soak time and hook depth), environmental (sea surface temperature), or biological variables (animal length) on the at-vessel hooking survival of sharks (binomial variable; dead/alive) caught as bycatch upon gear retrieval, we followed the methodology in Serafy et al. (2012) and used logistic regression to generate a model which was inclusive of all recorded variables which would likely affect catch/survival for each species. We applied the same model for each species without following a stepwise factor addition/removal methodology. The following model was applied separately for each species:

$$\mathrm{logit}(S) = \mathrm{Target} + \mathrm{Depth} + \mathrm{Soak} + \mathrm{Temp} + \mathrm{Length}$$

where S = Survival (0, 1 = dead, alive); Target = species targeted (tuna or swordfish); Temp = sea surface temperature (°C); Depth = maximum hook depth (in water column; m); Soak = soak duration (h); and Length = straight upper jaw/snout fork length (FL; cm).

Tunas are primarily targeted during the day and swordfish at night. We assigned the fishing target (tuna or swordfish) based on the proportion of light sticks to hooks used (swordfish, ≥ 0.7; tuna, < 0.4; all data < 0.7 and ≥ 0.4 were considered a "mixed target" and omitted from analysis). Fishes that were missing survival status, exhibited excessive soak times (i.e., > 24 h) and/or unrealistic temperatures (e.g., < 1 °C) were eliminated from analysis. All data used were recorded from 1995 to 2012. In 2004, the US National Marine Fisheries Service (NMFS) banned the use of J hooks in the US pelagic longline fishery, requiring all fishers to use circle hooks. To eliminate the influence of hook type in our analysis, we omitted any sets made prior to 2005 which used J hooks. Two variables which we were not able to incorporate directly into our models were hook size and degree offset. This is largely due to the lack of consistent measurement of these factors in the POP database; however, there is little variation in size for circle hooks across sets in the fishery (Serafy et al., 2012).

Species-specific least square mean survival estimates were used to determine shark survival rates. Mean survival rates were estimated for both swordfish- and tuna-directed sets. Species were also categorized according to their International Union for Conservation of Nature (IUCN) Red List status (The International Union for the Conservation of Natue, 2013) and the US National Marine Fisheries prohibited fishing target status (according to the POP database). Life history information on the reproductive traits of each species (female age at maturity and fecundity) were obtained from the reference tables within Cortés (2000, 2002) and Dulvy et al. (2008), as well as Hazin et al. (2000) using data from the Atlantic or Gulf of Mexico stocks of each species (in the rare case when these data were not available, other regions from the above papers were used as surrogates; parameters were averaged if a range was provided for a given species). Using these estimates, we ranked species according to their reproductive potential (lower fecundity and higher age at maturity = higher sensitivity), with higher rankings conferring higher risk, as the low-fecundity/low-natural mortality strategies of many elasmobranch fishes appear to render them less capable of population change than many teleost fishes (Myers and Worm, 2005; Stevens et al., 2000). We also scored each species' overall relative vulnerability to longline fishery bycatch by averaging ranks of age-at-maturity, fecundity, and mean survival between both tuna and swordfish sets (with higher survival = lower rank; each metric weighted similarly). Statistical analyses were performed using SAS (SAS Institute 1990) and statistical significance was declared at $p < 0.05$.

3. Results

3.1. Effects of fishery-related variables on survival

A total of 3431 swordfish and 1596 tuna sets were analyzed, with the number of observations per taxon ranging from 139 (longfin mako) to 17,780 (blue shark) for combined targeted sets. Estimated lengths ranged from 30 cm FL (shortfin mako and silky shark) to 480 cm FL (tiger shark, Table 1). Less than 1% of all captured sharks were classified as "damaged", and we removed these observations from our analyses to avoid confounding factors (i.e., the response variable would no longer be binomial). At-vessel survival was significantly affected by one or more independent variables in seven of the 12 species assessed (60%, Table 1). Statistically significant effects for fishing target (tuna/swordfish) were detected for four of the taxa assessed: blue (decrease), silky (increase), longfin mako (decrease), and night shark (decrease; Table 1). Furthermore, three species were significantly affected by soak time, with survival decreasing with increasing soak time for blue, porbeagle, and silky sharks (Table 1). Hook depth was a significant variable for four of the species analyzed, whereby positive relationships with survival were found for blue, night, and scalloped hammerhead sharks, and a negative relationship with survival for porbeagle shark (Table 1). Survival of four species was significantly affected by temperature, with inverse relationships detected for silky, blue, dusky, and night sharks (Table 1). Lastly, length was a significant factor affecting survival of 5 of 12 species: survival of silky, blue, dusky, and night shark significantly increased with body length, whereas it decreased with length for longfin mako (Table 1). Although it is not recommended to report R^2 values from fitted logistic regression models due to their routinely low values (Hosmer and Lemeshow, 2000), pseudo-R^2 value were generated following Shtatland et al. (2002) and presented in Table 1.

Table 1

Logistic regression results pertaining to the at-vessel survival for the 12 shark species encountered as bycatch during pelagic longline fishing as well as the regression coefficients for each variable: target (swordfish versus tuna sets), hook depth (m), temperature (°C), soak time (h), and length (Fork length, cm). Significant factors in bold. Pseudo R^2 values are also presented for each model.

Species/model	Intercept	*Target*	No. sets assessed (SWO/TUN)	*Hook depth*	Hook depth (mean ± SE)	*Temperature*	Temperature (mean ± SE)	*Soak time*	Soak time (mean ± SE)	*Length*	Length (mean ± SE)	Pseudo R^2
Bigeye thresher	0.90	ns	160/128	ns	49.17/0.79	ns	24.69/0.15	ns	8.21/0.10	ns	188.29/2.21	0.008
Blue	2.17	**−0.29**	955/385	**0.05**	23.11/0.07	**−0.023**	18.50/0.02	**−0.04**	8.23/0.01	**0.01**	149.31/0.29	0.024
Dusky	3.40	ns	105/44	ns	42.74/1.90	**−0.055**	25.42/0.20	ns	8.71/0.13	**0.01**	165.79/3.13	0.050
Longfin mako	−2.57	**1.01**	76/53	ns	44.47/1.64	ns	24.62/0.24	ns	8.65/0.17	**−0.01**	216.40/3.74	0.082
Night	2.78	**−0.74**	174/26	**0.05**	39.19/0.18	**−0.074**	25.86/0.11	ns	7.72/0.05	**0.02**	123.07/1.15	0.065
Oceanic whitetip	−5.72	ns	119/36	ns	47.04/0.88	ns	27.10/0.14	ns	7.57/0.13	ns	114.23/2.56	0.021
Porbeagle	3.73	ns	90/4	**−0.10**	18.17/0.44	ns	16.75/0.14	**−0.36**	7.80/0.08	ns	87.74/1.11	0.055
Sandbar	−5.15	ns	34/31	ns	34.75/0.97	ns	22.04/0.34	ns	8.75/0.13	**0.02**	147.09/2.23	0.040
Scalloped hammerhead	1.59	ns	121/79	**0.02**	45.90/0.61	ns	24.51/0.10	ns	8.10/0.07	ns	160.14/1.20	0.017
Shortfin mako	1.78	ns	514/336	ns	31.50/0.31	ns	21.42/0.08	ns	8.44/0.04	ns	137.57/0.98	0.002
Silky	1.64	**−0.72**	489/225	ns	46.54/0.33	**−0.021**	25.79/0.08	**−0.08**	8.27/0.05	**0.01**	121.55/0.99	0.068
Tiger	6.17	ns	594/249	ns	40.29/0.40	ns	25.27/0.08	ns	8.33/0.04	ns	217.67/1.57	0.008

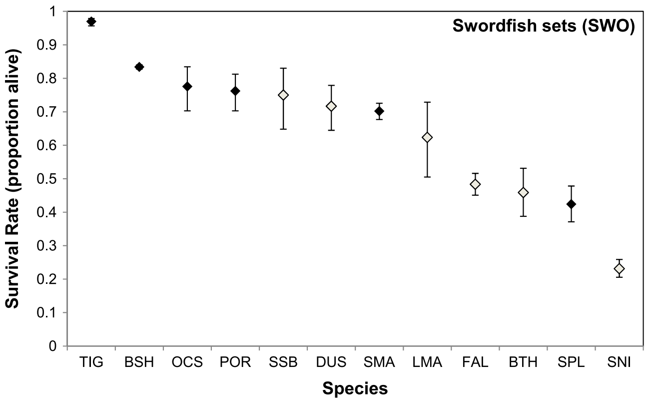

Fig. 1. Least-square mean survival estimates for 12 species encountered as bycatch in pelagic longline sets targeting swordfish. US National Marine Fisheries Service shark species identification codes are as follows: 'TIG' = tiger; 'BSH' = blue; 'OCS' = oceanic whitetip; 'POR' = porbeagle; 'SSB' = sandbar; 'DUS' = dusky; 'SMA' = shortfin mako; 'LMA' = longfin mako; 'FAL' = silky; 'BTH' = bigeye thresher; 'SPL' = scalloped hammerhead; 'SNI' = night. Gray dots indicate species prohibited from retention by pelagic longline gear as designated by the US National Marine Fisheries Service. Error bars represent the 95% confidence intervals. Fish classified as "damaged" were not included in the analyses and are thus not represented here.

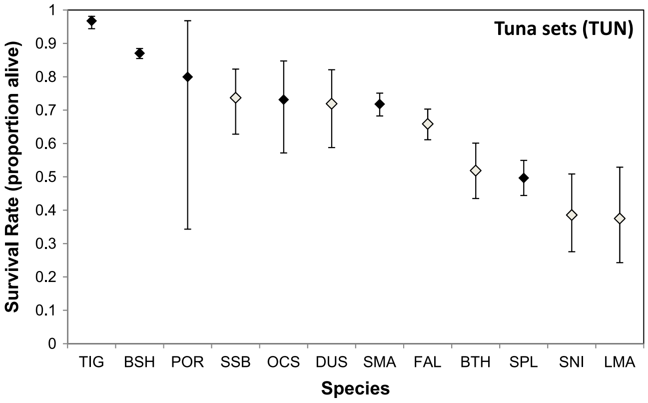

Fig. 2. Least-square mean survival estimates for 12 species encountered as bycatch in pelagic longline sets targeting tuna. US National Marine Fisheries Service shark species identification codes are as follows: 'TIG' = tiger; 'BSH' = blue; 'POR' = porbeagle; 'SSB' = sandbar; 'OCS' = oceanic whitetip; 'DUS' = dusky; 'SMA' = shortfin mako; 'FAL' = silky; 'BTH' = bigeye thresher; 'SPL' = scalloped hammerhead; 'SNI' = night; 'LMA' = longfin mako. Gray dots indicate species prohibited from retention by pelagic longline gear as designated by the US National Marine Fisheries Service. Error bars represent the 95% confidence intervals. Fish classified as "damaged" were not included in the analyses and are thus not represented here.

3.2. Survival estimates and reproductive capabilities

Least squares mean hooking survival rates varied between fishery targets and among species. In swordfish sets, survival was high for tiger (97.1%), blue (82.7%), and oceanic whitetip sharks (77.3%; Fig. 1), and lower for night shark (22.2%), scalloped hammerhead (42.3%), bigeye thresher (44.9%), and silky shark (49.4%; Fig. 1). Tuna-directed sets exhibited a similar pattern of higher survival for tiger (96.5%), blue (87.0%), and porbeagle sharks (82.7%, despite low sample size), and lower survival for night (43.8%) and longfin mako sharks (37.4%; Fig. 2).

Ranking species according to their reproductive capabilities (based on data from Cortés, 2000, 2002; Dulvy et al., 2008; Hazin et al., 2000) showed that the blue and oceanic whitetip shark had the youngest age at maturity, 5 and 5.5 years, respectively; (Table 2), whereas tiger, silky, night, and bigeye thresher sharks all were associated with moderate age at maturity rankings (8–12.7 years, Table 2). Conversely, four species were associated with older ages at maturity and thus rankings: porbeagle (13 years), scalloped hammerhead (15 years), sandbar (15.5 years), shortfin mako (∼19 years), and the dusky shark (19 years). High fecundity (number of pups per litter per year) translated into low rankings for tiger (55 pups, ranked lowest), blue (37 pups, 2nd lowest), and scalloped hammerhead sharks (35 pups, 3rd lowest). Higher sensitivity was evident for species with few pups per litter such as the dusky (9 pups, 7th), the sandbar (8 pups, 8th), porbeagle (4 pups, 9th), and bigeye thresher (3 pups, 10th). A continuum of overall relative vulnerability (average of mean survival, age at maturity, and fecundity rankings) among species emerged which appeared to cluster certain groups of species: tiger, blue, and oceanic whitetip sharks exhibited low vulnerability, whereas the night, scalloped hammerhead, shortfin mako, dusky, bigeye thresher, and longfin mako emerged the most vulnerable to longline bycatch mortality (although the latter species should be treated with caution due to lack of life-history data; Figs. 3 and 4).

Table 2
Species attributes and their respective overall relative vulnerability rankings (lower ranking = lower vulnerability).

Species	Age at maturity (years)	Maturity ranking	Fecundity (offspring/year)	Fecundity ranking	No. observed alive	No. observed dead	Mean survival rate	Mean survival rank	Vulnerability ranking
Longfin mako	18.5[a]	10	3	10	73	66	48.9	9	9.7
Bigeye thresher	12.7[b]	6	3[b]	10	178	189	48.3	10	8.7
Dusky	19	11	9	7	193	81	72.1	6	8.0
Sandbar	15.5	9	8	8	138	51	73.3	5	7.3
Scalloped hammerhead	15[b]	8	35[b]	3	336	391	45.9	11	7.3
Shoftfin mako	18.5	10	12.5	5	1503	623	71.4	7	7.3
Night shark	10[b]	5	15	4	292	849	33.0	12	7.0
Porbeagle	13	7	4	9	193	62	78.6	3	6.3
Silky	9.5[b]	4	10	6	1004	86	57.8	8	6.0
Oceanic whitetip	5.5[b]	2	12.5	5	162	51	74.3	4	3.7
Tiger	9	3	55	1	1305	43	96.8	1	1.7
Blue	5	1	37	2	14788	2992	84.9	2	1.7

Age at maturity and fecundity estimates were derived from the appendices used in Cortés (2000, 2002) and Dulvy et al. (2008) corresponding to stocks from the Northwest Atlantic unless otherwise noted (with a 'b').

[a] Due to a lack of data on longfin mako age at maturity, we used the same data as the shortfin mako.

[b] Symbols refer to regions used for that particular measure: bigeye thresher = Northeast Pacific (age), Northeast Atlantic (fecundity); night = Southwest Atlantic from Hazin et al. (2000); oceanic whitetip = Atlantic and Pacific; scalloped hammerhead = Northwest Gulf of Mexico (age + fecundity); silky = Northwest Gulf of Mexico.

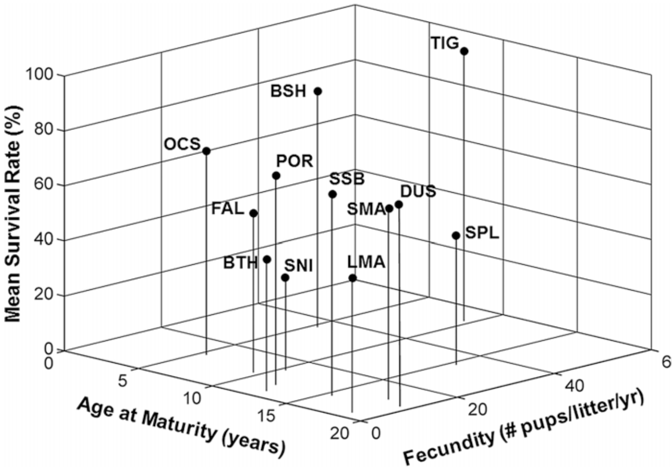

Fig. 3. Interaction plot showing mean survival rate (%, swordfish and tuna combined), age at maturity (in years), and fecundity (# of pups per litter per year) for each species. US National Marine Fisheries Service shark species identification codes are as follows: 'TIG' = tiger; 'BSH' = blue; 'OCS' = oceanic whitetip; 'POR' = porbeagle; 'SSB' = sandbar; 'DUS' = dusky; 'SMA' = shortfin mako; 'LMA' = longfin mako; 'FAL' = silky; 'BTH' = bigeye thresher; 'SPL' = scalloped hammerhead; 'SNI' = night.

4. Discussion

4.1. The impacts of bycatch

It is estimated that bycatch represents a major threat to over 70% of elasmobranch species (Molina and Cooke, 2012) and there is mounting evidence that populations of elasmobranchs subjected to bycatch can decline over short time scales (decades; Casey and Myers, 1998; Baum and Myers, 2004). The responses of individuals to the process of hook-and-line capture can vary highly among species (Mandelman and Skomal, 2009; Gallagher et al., 2014b), leading to differences in acute (maintenance of physiological equilibrium, Frick et al., 2010) and long-term (survival and reproductive fitness) consequences.

This study is one of the first attempts to investigate the effect of fishery target on shark bycatch survival in pelagic longline fisheries, and we found it to be significant for one-third of the species assessed. For 7 of the 12 (58%) species, we rejected the null hypothesis of no influence of fishery-related variables on shark survival (Table 1). Survival was significantly lower for blue, night and silky sharks in swordfish sets. Swordfish directed sets are often made at sunset to take advantage of the fact that swordfish feed near the surface at night. Blue and silky sharks, and to a lesser extent, night sharks, are medium-bodied, ram-feeding species that also forage on prey species that ascend to the surface at night (Bonfil, 2008; Nakano and Stevens, 2008). Due to individuals already expending energy during food acquisition, as well as the social stress

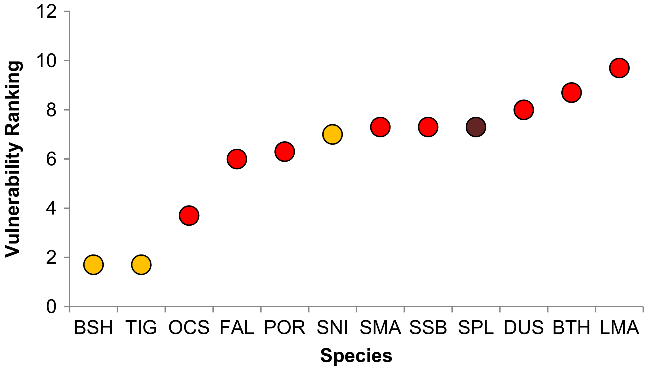

Fig. 4. Overall relative vulnerability scores for all of the shark species assessed. Each score was obtained by averaging the sensitivity rankings of species survival rate (swordfish and tuna combined), age at maturity, and fecundity (see Table 2). Increasing vulnerability confers a higher overall relative risk to bycatch. Colors signify species-specific IUCN Red List category [47]: orange = "Near Threatened;" red = "Vulnerable;" maroon = "Endangered". US National Marine Fisheries Service shark species identification codes are as follows: 'BSH' = blue; 'TIG' = tiger; 'OCS' = oceanic whitetip; 'FAL' = silky; 'POR' = porbeagle; 'SNI' = night; 'SMA' = shortfin mako; 'SSB' = sandbar; 'SPL' = scalloped hammerhead; 'DUS' = dusky; 'BTH' = bigeye thresher; 'LMA' = longfin mako. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

resulting from competition, we hypothesize that the process of being captured and subsequently fighting on a longline may synergistically result in additive metabolic and physiological burdens resulting in higher rates of mortality for these species.

4.2. Physiological effects

Temperature is a major controlling factor in the behavior, growth, and life history of most fish species. However, the interaction among water temperatures, fishery capture stress and survival is poorly understood, particularly in bycatch scenarios for marine fishes (Davis, 2002; Gale et al., 2013). Warmer water temperatures typically contain lower amounts of dissolved oxygen and can increase the metabolic rate and magnitude of capture stress in sharks (Skomal and Bernal, 2010). Our data indicated that the survival of blue, dusky, night, and silky sharks – all ectothermic species – significantly decreased with increasing temperature. Survival showed a significant increase at deeper hook depths for blue, scalloped hammerhead and night sharks supporting the notion that access to deeper, cooler waters may limit oxygen deficits when captured (Table 1). An additional factor which could influence survival due to asphyxiation is soak times of the gear, which may be prolonged when captured on short gangions (which limit ram-ventilation) during commercial longline fisheries. Blue, porbeagle, and silky sharks exhibited decreasing survival with increased soak time in our study (Table 1). Collectively, these results suggest that elevations in water temperature and soak time could significantly decrease the survival of some sharks captured as bycatch in pelagic longlines, and that avoiding fishing during times/seasons with warmer water temperatures, and/or setting hooks in cooler, deeper water may be tactics for mitigating shark stress and mortality associated with fishing (Hoffmayer et al., 2012). This would presume that captured individuals would not suffer barotrauma as seen in teleosts, whereas the feasibility of a change in fishing tactics would depend on the effect it would have on fish catches of targeted species. Furthermore, while temperature here is treated as a linear factor, future work might explore the possibility of species-specific temperature thresholds that dictate survivability.

Temperature changes can also result in other sublethal effects on fishes (e.g., physiological disturbance, behavioral changes, reproductive loss; Cooke et al., 2002). These fitness losses may be of special concern for large and/or fecund individuals, as previous work has shown that temperature and other stresses of capture function to interrupt endocrine systems and processes associated with reproduction (Barton and Iwama, 1991; Pankhurst and Dedual, 1994). Furthermore, while there is considerable uncertainty as to the effects of anthropogenic climate change on marine systems (Hoegh-Guldberg and Bruno, 2010), the potential of warming sea temperatures may exacerbate the above relationships between elevated temperatures and shark survival as bycatch.

4.3. Stress and exhaustion

Fish metabolic processes often scale with body size (Clarke and Johnston, 1999; Dowd et al., 2006). Recent evidence suggests that as sharks increase in size, they may become more resistant to the physiological consequences of fisheries capture (Gallagher et al., 2014b). Our results are in agreement with this study for blue, dusky, silky, sandbar and night shark (Tables 1 and 2). Interestingly, these five species share body plans that lack unique morphological structures (as seen in other species, such as the hammerhead's cephalofoil and the thresher's tail) and they generally attain smaller maximum sizes than some of the other species in our study (i.e., tiger, thresher). Moreover, the survival of this complex of species (blue, dusky, silky, sandbar, night) was affected similarly by the suite of factors examined. The diversification of body plans is one of the most important factors leading to evolutionary divergence, and how specialization of key traits (morphological and functional) in captured fishes affects their subsequent survival is an area deserving of future study (Gallagher et al., 2014a).

Tiger sharks were ranked the most robust species to bycatch mortality in our study, exhibiting ∼97% at-vessel survival in both swordfish and tuna sets (Figs. 1 and 2), and, when considering their high fecundity and relatively low age at maturity, this species received one of the lowest overall relative vulnerability rankings (Table 2). Their apparent tolerance to capture stress is consistent with other work documenting minimal physiological disruption on fishing lines (Mandelman and Skomal, 2009; Gallagher et al., 2014b) and very low (2%–8%) mortality in pelagic and bottom longlines (Beerkircher et al., 2002; Morgan and Burgess, 2007; Morgan and Carlson, 2010). Blue sharks and sandbar sharks were also ranked as relatively robust against bycatch mortality, and are both known to resist physiological disturbance (metabolic and respiratory acidoses; Brill et al., 2008; Campana et al., 2009). However, the differences in reproductive rates between these species alter their relative vulnerability to bycatch (Figs. 2 and 3): blue sharks reach maturity nearly three-times faster and produce about four-times as many pups per litter than sandbar sharks, resulting in a higher vulnerability to bycatch for the sandbar shark.

4.4. *Vulnerability*

Species in the present study are clustered in groups according to their vulnerability (Fig. 3). Silky sharks, which were found to have the highest degree of vulnerability in a 2010 International Commission for the Conservation of Atlantic Tunas (ICCAT) ecological risk assessment for Atlantic sharks (ICCAT, 2011), displayed moderate survival in tuna sets, but low survival in swordfish sets, which resulted in moderate-to-low survival rankings and a moderate vulnerability ranking. Mean survival rates of bigeye thresher, scalloped hammerhead and night sharks were the lowest of the 12 species assessed (Fig. 3). Despite the relatively high fecundity of the scalloped hammerhead (Cortés, 2000, 2002), its slow attainment of maturity and low survival render it more vulnerable to bycatch (Table 2, Fig. 4); bigeye thresher sharks display similar values in survival and age at maturity, but much lower fecundity. Both of these species are phylogenetically divergent and morphologically specialized: thresher sharks have evolved an elongated upper-lobe of the caudal fin used in prey capture (Oliver et al., 2013); whereas hammerhead species possess a distinctive cephalofoil which is thought to afford enhanced sensory capabilities (McComb et al., 2009). The shape of an animal has a direct effect on how they exchange energy and materials with their surroundings, and functional specialization is often tied to the concept of 'trade-offs' (Irschick et al., 2005; Gallagher et al., 2014a). As mentioned earlier, species with basic body plans were actually afforded higher survival as they attained larger sizes. However, whether these specialized structures may have resulted in trade-offs that reduce survival upon capture (i.e., smaller mouths resulting in limited oxygen update during fighting) remains unknown.

4.5. *Risk assessment*

Survival assessments, such as the one employed here, may help predict the susceptibility of sharks to exploitation over long time scales. For example, a fishery-independent shark survey conducted off Florida's coast in the early 1980s found that scalloped hammerheads were among the top three most common species (Berkeley and Campos, 1988), but have been subject to an estimated annual rate of change of −20% since 1992 (Baum et al., 2003). In the Northwest Atlantic, scalloped hammerheads suffered a nearly 90% decline between 1986 and 2000 (Baum et al., 2003). In our study, we found that scalloped hammerheads exhibited among the lowest survival rates as bycatch (Table 2). When considering the findings from the above time-series, we suggest bycatch capture likely played an important role in the decline of this species. This point is supported by that fact that populations of species that exhibited high tolerance to bycatch in our study (i.e., tiger) may be stabilizing or increasing in recent years in the Northwest Atlantic (Baum and Blanchard, 2010; Carlson et al., 2012), suggesting that life-history parameters in isolation do not explain overharvest. That said, the rankings of overall relative vulnerability used in the present study may not reflect the susceptibility of shark stocks to exploitation throughout the Atlantic Ocean if a small proportion of the stock is present where the majority fishing occurs, or if the abundance of the species in question is very high. While performing an Atlantic-wide stock assessment to vulnerability from bycatch is beyond the scope of this study, future work could employ spatial analyses using data from the many national fishing fleets operating in the Atlantic and examine vulnerability based on catch, effort and susceptibility (e.g., probability of encounter). Furthermore, we recognize that other measures such as maximum body size, maximum age, and growth rates are valuable measures of resilience of fishes to exploitation; we used age at maturity and fecundity because they are both recognized among the most important biological predictors of extinction risk and these standardized metrics are easily comparable among species (Reynolds et al., 2005).

Our results also suggest that, broadly, the IUCN Red List (The International Union for the Conservation of Natue, 2013) categories accurately reflect the overall relative vulnerabilities of the 12 species examined in this study (Fig. 4). For example, the two least vulnerable species (blue and tiger sharks) were listed as "Near Threatened" by the IUCN, and three of the most vulnerable species (bigeye thresher, dusky, and night shark, excluding longfin mako due to data limitations) were all listed as "Vulnerable". Silky sharks exhibit moderate overall vulnerability to pelagic longline bycatch and appear to be properly listed as "Near Threatened", whereas the oceanic whitetip displayed low overall vulnerability yet are listed as "Vulnerable" globally and "Critically Endangered" in our study area. These differences suggest that the existing risk categorization of species may be augmented by survival assessments and that interactions with other fisheries (e.g., incidental captures in trawls or direct harvest) or combinations of other extrinsic factors (gear changes, species misidentification) may better explain the reported extreme declines than bycatch in pelagic longline fisheries for certain species (i.e., oceanic whitetip).

5. Conclusions

While bycatch has been cited as a major driver of extinction risk for pelagic shark species, it clearly does not affect all species similarly. Moreover, longline bycatch mortality has differential explanatory power in framing the population declines (and risks) of certain species, as evidenced by the large gradient in vulnerability that we documented. For those species which are most affected, however, our study agrees with the notion that the best conservation strategy may be to reduce shark interactions with fishing gear (e.g., time–area closures) because solely restricting harvest or discarding captured individuals will not eliminate mortality if sharks are already dead upon gear retrieval (Gilman, 2011; Jordan et al., 2013). In addition to restricting longline fishing where species susceptible to bycatch mortality occur, other strategies that show some promise for altering species-specific vulnerabilities to capture may include setting lines in deeper water, altering the bait used, and employing sensory based deterrents (Gilman, 2011; Jordan et al., 2013). For example, Rigg et al. (2009) found that scalloped hammerhead sharks (a species we found to exhibit among the lowest at-vessel survival) avoided the magnetic fields of magnets placed on fishing gear, while Hutchinson et al. (2012) found the use of lanthanide metals on longline hooks reduced the catch of scalloped hammerhead sharks.

Studies on fish species have been traditionally slower to link ecology and evolution to risk of extinction when compared to their terrestrial counterparts (Reynolds et al., 2005). However, the need to consider the phenotypic and adaptive responses when predicting survival outcomes, especially marine fishes threatened with extinction, is gaining recognition (Young et al., 2006; Gallagher et al., 2014a). Our study adds to the growing body of literature that provide suggestions for reducing bycatch mortality to threatened species (e.g., setting in deeper water, time–area closures, using species-specific deterrents). Moreover, our work suggests that the historical selection of biological and ecological traits may have disparate consequences when species are exposed to fishery stressors. Accordingly, consideration of species' ecological and evolutionary variables in addition to survival rates and life-history parameters may be useful in determining which management strategies offer the most effective conservation benefits in the future.

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