Ecological interactions between 19 shark species in the Indian Ocean

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Abstract

Apex predators such as sharks are a critical component of ocean ecosystems. Yet the ecosystem consequences of shark declines remain poorly understood, primarily because of a lack of population and community baselines. The Indian Ocean is especially data-poor in ecological data, and even moreso in historical data. We utilized a longline survey dataset from 1966 through 1989 that spanned the majority of the Indian Ocean and recorded 19 shark species. This time period corresponds to the start of large-scale industrial fishing in the region. Trends across the species were highly variable; life history and fishing pressure metrics were not able to explain differences in responses between species, suggesting that changes in ecological interactions such as competition and predation had a prevalent role historically. To further explore ecological interactions between the species, we conducted a literature review of the study species' diets with a focus on intra-guild predation. We constructed an interaction web to identify keystone species. Several species were neither predator nor prey of other sharks, suggesting that competition may be the more salient relationship to other sharks. Overall, species with broader habitat preferences and smaller individuals are now a larger part of the pelagic shark community, whereas open-ocean species have declined. These results suggest that industrial fishing restructured shark communities and diminished the top-down control of sharks in pelagic ecosystems.

Introduction

Sharks are crucial to the structure and function of marine ecosystems (Heupel, Knip, Simpfendorfer, & Dulvy, 2014). Their roles extend across the world's oceans and often through multiple ecosystems via their spatial migrations, broad selection of prey species, and diving behaviors (Bird et al., 2018; Andrzejaczek et al., 2022). The life history traits that enable sharks to inhabit their ecological niche, such as their large body size, also make them highly vulnerable to anthropogenic disturbances. In addition to direct targeting, heavily fished ocean regions tend to be shark biological hotspots (Queiroz et al., 2019; T. D. White et al., 2019). Since the start of large-scale commercial longlining in the 1950s, many populations have experienced large declines in abundance and decreases in average body size (Ward & Myers, 2005; Dulvy et al., 2008; Pacoureau et al., 2021).

Sharks have received attention in fisheries management and conservation only in recent decades (Ferretti, Worm, Britten, Heithaus, & Lotze, 2010). Accurate, species-level shark data are rare (Clarke et al., 2006), and local knowledge is often lost as one generation of fishers replaces the next (Sáenz-Arroyo, Roberts, Torre, Cariño-Olvera, & Enríquez-Andrade, 2005). This, and the fact that, until recently, they were difficult to study due to their migratory capacity to move far offshore and into great depths, have resulted in shark population baselines being poorly understood. Yet, setting benchmarks are vital to inform policy interventions (Engelhard et al., 2016). Policies that do not consider historical data often underestimate extinction risk and set higher fishing quotas (McClenachan, Ferretti, & Baum, 2012). As a result, shark populations are largely not managed at levels that ensure sustainable exploitation (Davidson, Krawchuk, & Dulvy, 2016; Dulvy et al., 2017).

The Indian Ocean is one of the least studied ocean sectors for shark exploitation and bycatch (Molina & Cooke, 2012), posing a significant challenge for sustainable management. Four of

the top ten shark-fishing countries border the Indian Ocean (Brautigam, 2020), yet the region lacks the data needed to adequately manage their fisheries (van der Elst et al., 2009). In addition to historical data deficiencies, sharks can be difficult to identify to the species level when caught. The Indian Ocean Tuna Commission's (IOTC – the regional managing body of high-seas fisheries) publicly available catch data only contains four shark species and two aggregated genera. Only one species monitored by the IOTC—the blue shark (*Prionace glauca*)—has enough data to conduct a full stock assessment (*Executive Summary: Blue Shark (2020)*, 2020). A recent synthesis of global oceanic shark trends (Pacoureau et al., 2021) had large taxonomic and spatial gaps in the Indian Ocean, as it relied heavily on spatially limited datasets from South Africa and Western Australia. The countries bordering the Indian Ocean are home to a third of the world's population and are especially reliant on their fisheries, as many are developing nations that depend on seafood as a primary source of protein (Roy, 2019). Issues of management thus become issues of nutrition security and food justice as well.

Here, we use historical ecological methods to establish population baselines for sharks in the Indian Ocean utilizing data from a scientific longline survey conducted throughout the region from 1966 to 1989 (Fig. 1). The historical longline survey was conducted by USSR scientists using gear targeting tuna (Romanov, Sakagawa, Marsac, & Romanova, 2006). USSR scientists measured, weighed, and identified sharks caught to the species level (Romanov et al., 2006). The level of species detail in the survey data is unparalleled for the region. Additionally, the USSR survey covers the beginnings of industrial longlining in the Indian Ocean. Pelagic shark stocks in the Indian Ocean were thought to be near-pristine in 1971, five years after the start of the USSR survey (Brunel et al., 2018). While Japan and Taiwan started exploiting these waters in a limited capacity shortly before the survey began, twenty other nations eventually joined (Fonteneau, 2017), along with significant improvements in longline gear and refrigeration technology (Ward & Hindmarsh, 2007). Industrial purse seining began in the Indian Ocean in the

late 1970s (Fonteneau, 2017), and both longline and purse seine catches rapidly scaled up in the 1980s (Miyake, Miyabe, & Nakano, 2004). The 1980s also saw the start of direct targeting of sharks by commercial fisheries due to increased global demand for shark fins (Camhi, Valenti, Fordham, Fowler, & Gibson, 2009; Fabinyi, 2012). The aforementioned historical USSR survey therefore gives a crucial insight into Indian Ocean shark populations at pre-industrial fishing levels, and follows them through increasing fishing pressure to 1989. Hence, this analysis allowed us to characterize large-scale human impacts on Indian Ocean sharks over the majority of their industrial exploitation history and to explore drivers and ecosystem consequences with an unprecedented level of taxonomic, spatial, and temporal resolution.
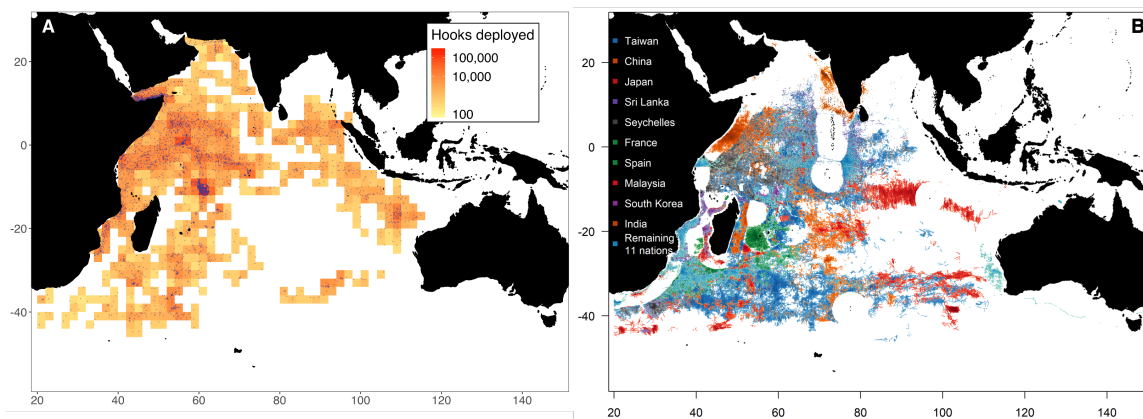
Fig. 1. (A) USSR survey effort by number of hooks (2° by 2° resolution). Purple dots are locations of longline sets. (B) Fishing hours by longliners determined by Global Fishing Watch in the IOTC's area of competence in 2019 (0.1° by 0.1° resolution).

Methods

We estimated historical catch rates from a scientific longline survey carried out by the former Soviet Union (USSR). Longline sets were cast throughout the Indian Ocean between 1961 and 1989 as part of the Soviet Indian Ocean Tuna Longline Research Programme (SIOTLLRP) (Romanov et al., 2006). We used a zero-inflated negative binomial (ZINB) generalized additive

model (GAM) to generate catch per unit effort (CPUE) models for the 19 species identified in the survey. Details of these models can be found in IOTC-2023-WPEB19-20.

We tried to explain the variation in abundance trends between species first with variables traditionally associated with population dynamics models. These fell into two categories: life history traits relating to population growth and exposure to fishing relating to mortality. We used the R package "rFishBase" to find life history traits for the species (Boettiger, Temple Lang, & Wainwright, 2012). In additional to metrics developed by Murua et al. 2018, we quantified exposure to fishing using publicly available IOTC catch and effort data (Commission, 2021).

To test the relationships between species in the data, we predicted the CPUE for each species at each set in the survey. We then generated new pairwise ZINB GAM models for each species with the abundance of each other species as an explanatory variable and recorded the model's parameter estimate of the effect of the species:

$$\text{species A} \sim \text{original species A model parameters} + \text{species B}$$

Further, we conducted two literature reviews to gather information on possible predator-prey and competitor relationships between the shark species in this study. We first searched Web of Science for the diets of the study species using the query "([common name] OR [scientific name]) AND diet". From the resulting papers, we recorded which of the study species were found in that species' diet, and the percentage of stomach contents by mass of both elasmobranchs and selachimorphs.

In a second review, we used the query "([common name] OR [scientific name]) AND compet*" in Web of Science to find any competitive relationships between the study species. We noted these with a binary variable, giving a pair of species a score of 1 if a paper any likely competition. Papers were included if they tested a hypothesis related to interspecific competition—papers that only discussed competition as a possible explanation of the observed

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results were not included.

Results

Standardized abundance trends

Seven species and four genera were caught frequently enough in the USSR survey to produce a standardized catch per unit effort (CPUE) time-series (Fig. 2A - K). We took the count process of the ZINB GAM as a proxy of abundance, and its instantaneous rate of change (IRC) over time (the model's year coefficient) as a proxy of the species' change in abundance over the survey period. Of the 19 total species, five had a significantly positive IRC in the count process, nine had significantly negative IRCs, and five had a non-significant IRC (Fig. 2L).
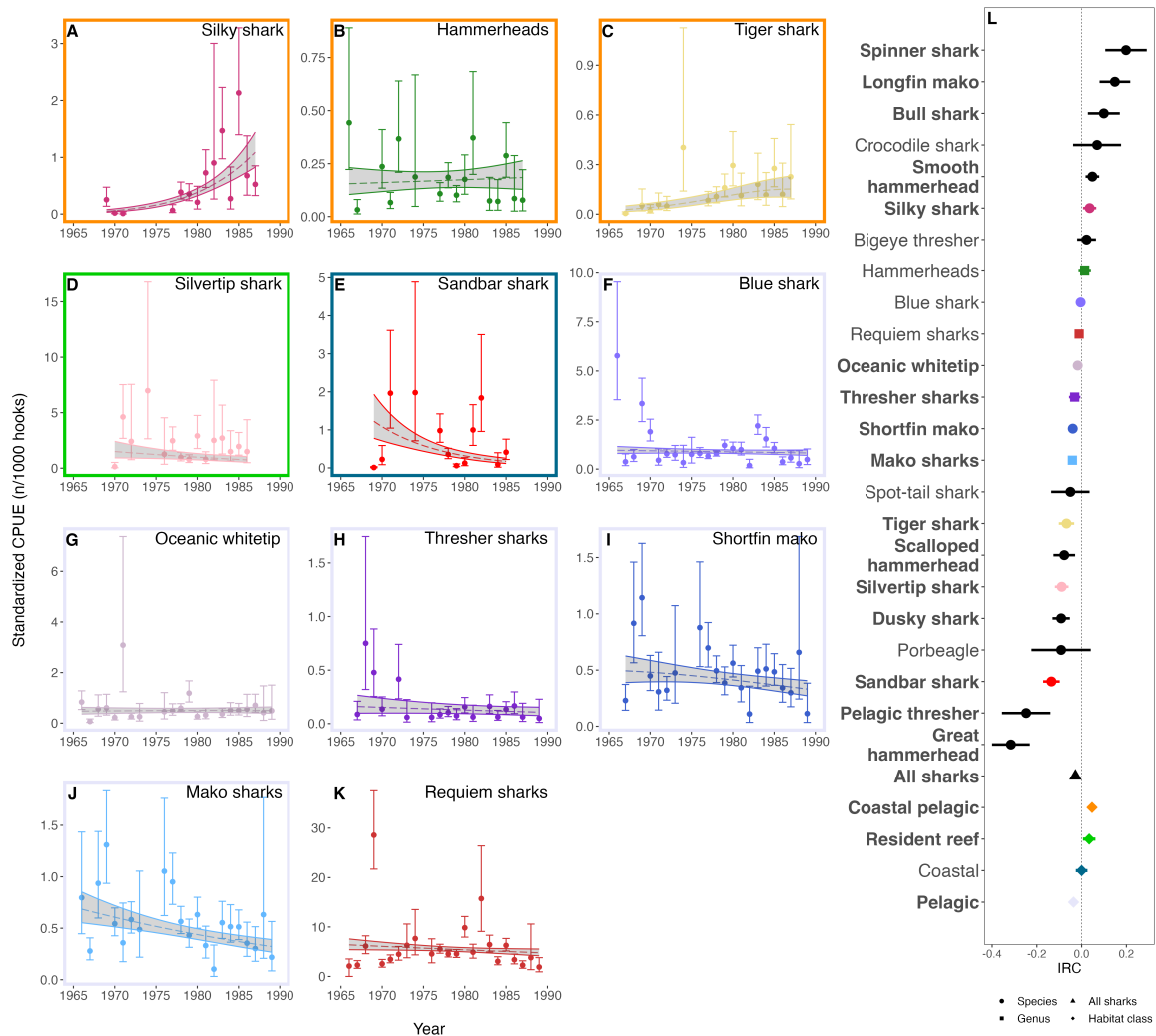
Fig. 2. Standardized CPUE time-series for (A) silky shark (*Carcharhinus falciformis*) (B) the hammerhead genus *Sphyrna* spp., (C) tiger shark (*Galeocerdo cuvier*), (D) silvertip shark (*C. albimarginatus*), (E) sandbar shark (*C. plumbeus*), (F) blue shark (*Prionace glauca*), (G) oceanic whitetip (*C. longimanus*), (H) thresher shark genus *Alopias* spp., (I) shortfin mako (*Isurus oxyrinchus*), (J) mako shark genus *Isurus* spp., (K) requiem shark genus *Carcharhinus* spp. Border colors of CPUE series represent the habitat group of the species or genus. (L) Instantaneous rate of change (IRC) of abundance over time in the count process. Bolded species names on the y axis had significant trends in abundance.

To explore changes in community composition, we divided the species into four major groups according to their habitat preferences. Coastal-pelagic species—species that spend significant amounts of time in both open ocean and nearshore habitats—experienced the greatest

increase in abundance, 67.2% (95% C.I. 47.9 - 79.4%; Fig. 2L). Reef resident species also increased by 54.0% (95% C.I. 12.5 - 75.8%), while coastal species remained relatively unchanged (-0.1% 95% C.I. -45.1 - 44.9%). Pelagic, or open ocean, species were the only group with a significant decline in abundance over the survey period, at -58.0% (95% C.I. -47.1 - -66.6%). The coastal, pelagic, and coastal-pelagic groups all contained species with both significantly increasing and decreasing individual abundance trends.

Drivers of abundance trends

Vulnerability to fishing

To explain why some species increased while others declined during the USSR survey, we tested nine proxies of species vulnerability to fishing. Of these, only lifespan had a significant relationship with abundance trends (Fig. 3A), correlating negatively with species' changes in abundance over the USSR survey period. Variable transformations and removing outliers did not produce statistical significance for any of the other variables. Other measures of life history traits suggestive of vulnerability to fishing varied in their relationship with the abundance trends. The maximum growth rate Rmax, an overall measure of species resilience, correlated positively with the species' abundance trends (Fig. 3B). The maximum length of each species correlated negatively with species' abundance trends (Fig. 3C). Trophic level correlated positively with abundance trends (Fig. 3D). The species' trend in size over the survey correlated negatively but not significantly with its trend in abundance (Fig. 3E).

Measures of exposure to fishing (Fig. 3F-I)—longline availability, longline susceptibility, average susceptibility, and hooks-per-meter-squared in habitat—all correlated positively with abundance trends. Availability refers to the amount of overlap between a species' habitat and a fishery; susceptibility is an overall estimation of the impacts of a fishery on a species that incorporates availability (Murua et al., 2018). Additionally, a linear model with both Rmax and

longline susceptibility as explanatory variables did not find a significant relationship with the species' trajectories.
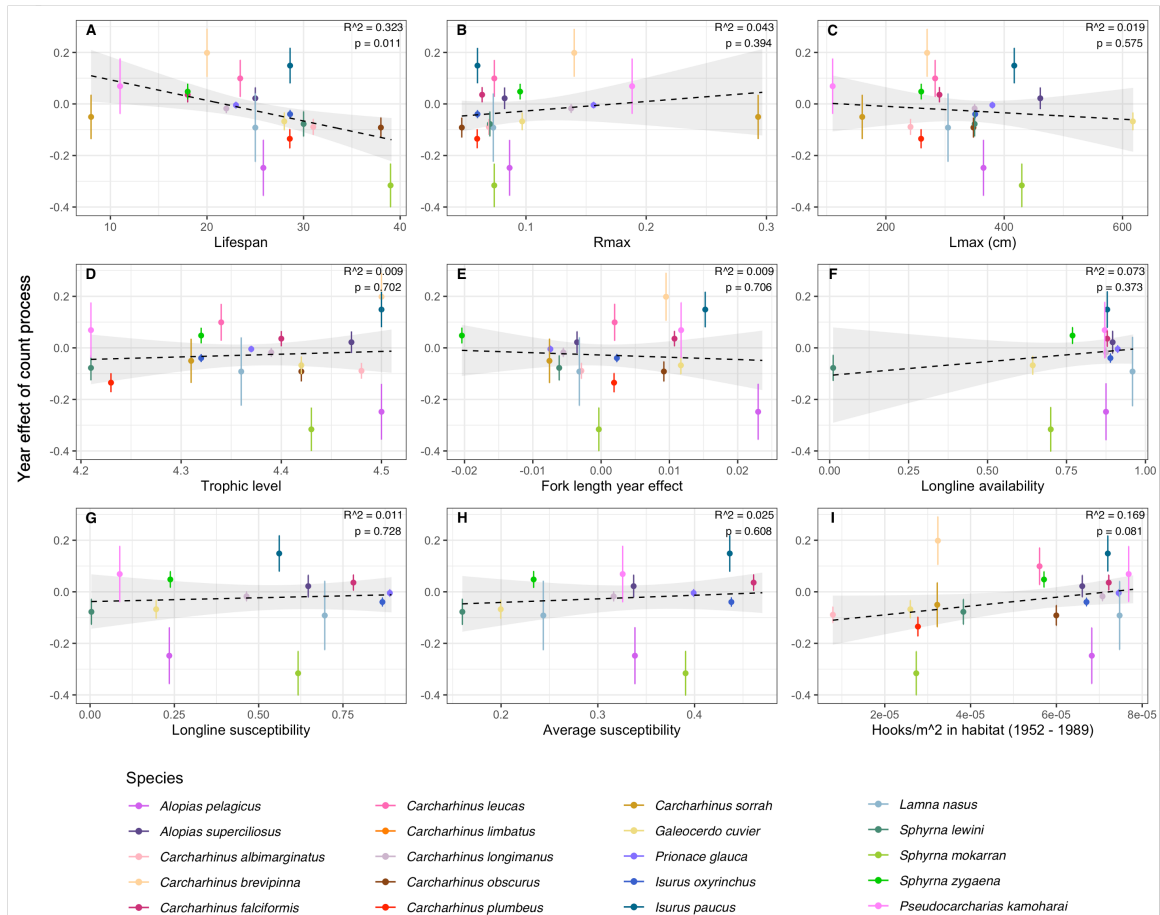
Fig. 3. True abundance trend from the USSR survey regressed against (A) lifespan; (B) the maximum growth potential, Rmax; (C) maximum length; (D) trophic level; (E) species' trend in size over time in the USSR survey; (F) spatial overlap between longline gear and species habitat (Murua et al., 2018); (G) overall susceptibility to longline gear (Murua et al., 2018); (H) average susceptibility to longlines, purse seines, and gill nets (Murua et al., 2018); and (I) concentration of hooks in each species' habitat, calculated from the IOTC database, from 1952 to 1989.

Species model effects

As zero-inflated models are mixture models of a count process and zero process, it does not generate overall variable parameter estimates, but estimates for each component model separately. The count process models the underlying ecological factors driving catch, such as the abundance of the species and the chances of it being in a feeding mode to bite the hook. The zero process models structural processes causing excess zeros, such as flaws in sampling methods. Therefore, we include in Table 1 the estimates from the count process of the table.

	pth	bth	als	ccb	fal	cce	ocs	dus	ccp	ccq	tig	bsh	sma	lma	por	spl	spk	spz	psk
pth		0.34	-1.3	-0.02	0.42	2.14	-8.07	-6.65	-2.99	-29.85	-3.22	0.17	0.42	51.99	-321995.81	-14.89	-17.87	-18.04	-243.68
bth	-5.63		0.18	0	-0.92	8.08	2.6	0.54	0.11	3.39	0.31	-1.04	-3.16	-0.31	-21.54	0.23	-0.2	5.7	-6.9
als	17.15	2.9		0	1.03	-3.3	0.74	-0.13	-0.09	-0.22	-0.38	-1.79	2.57	19.18	-938.96	5.43	-0.69	-2.16	-16.02
ccb	-74.28	-1.08	-0.1		0.47	-5.27	-1.98	-2.7	-0.93	-0.94	-2.55	0.12	2.38	61.07	-903.32	17.28	-9.07	-4.32	-86.6
fal	-13.99	-1.71	0.01	0		2.73	0.89	-0.06	-0.66	-0.08	-1.33	-1	-0.43	-3.68	-21.24	-2.28	-2.1	-2.43	-4.87
cce	-56.74	-19.31	0.49	0	1.01		0.7	0.25	0.68	0.22	3.66	-1.11	-5.17	-28.56	-707.92	-9.01	1.74	-4.39	-20.83
ocs	-3.07	-0.88	-0.02	0	-0.13	-3.46		-0.34	-0.06	-0.39	-0.32	-0.21	-0.55	3.9	-11.64	-0.39	0.38	-0.11	0.93
dus	5.08	0.09	0.01	0	0.2	-3.04	-1.48		0.08	-2.07	0.56	-1.45	-0.23	20.16	-11.21	0.93	0.43	-0.38	-1.12
ccp	-85.87	-8.06	-0.09	0	0.22	-0.1	-6.59	-1.29		-0.36	-1.02	1.04	-2.35	30.76	-407.09	2.53	-3.26	-1.37	-32.57
ccq	-6.07	0.41	-0.11	-0.27	-2.08	2.75	-5.34	-0.83	-0.36		-0.85	2.91	0.33	-9.91	-1163.23	-2.52	-1.61	0.43	9.93
tig	2.9	-0.06	-0.07	0	0.22	-5.11	-0.03	-0.4	-0.02	-0.13		-2.11	0.25	-9.06	-480.67	-0.41	-1.8	-0.67	-2.77
bsh	12.86	1.13	-0.08	0	-0.38	-4.29	-0.29	0.26	-0.44	-0.89	-0.72		0.65	-1.48	2.66	1.06	0.01	0.04	-0.15
sma	-5.54	0	-0.01	0	0.08	3.14	-0.41	-0.05	0.03	0.06	-0.1	-0.28		-2.45	-1.54	-0.08	-0.72	2.18	-1.34
lma	-16.06	-0.04	-0.02	0	-0.56	-6.47	1.93	-0.26	-0.28	-9.38	-0.76	2	-1.61		-62.5	-0.5	-2.01	-10.79	-0.86
por	-3.2	0.19	0.06	-0.73	-18.71	3.1	7.37	-0.98	0.31	0.56	-0.1	-0.06	2.38			-33.82	-1.37	1.54	7.08
spl	-3.71	0.04	0.02	0	-0.35	-22.35	0.06	-0.01	-0.06	-2.45	-0.24	1.45	-0.23	2.37	-0.72		0.81	-2.85	1.44
spk	-27.44	-7.21	-0.03	-0.2	-0.5	-7.03	-3.99	-0.37	-0.07	-0.11	-0.25	-1.08	-2.38	4.46	-458774.38	14.8		-2.51	-21.83
spz	-0.91	0.25	0.42	0	0.01	-0.24	0.6	-0.34	-0.03	0.1	0.31	-0.34	-0.26	-10.9	-15.82	0.49	-3.99		-17.24
psk	-549.42	-18.3	-0.83	0	-8.02	-32.73	-6.59	-3.58	-7.32	-27.59	-5.48	0.01	-7.79	-15.75	378.22	-5.52	-0.78	7.21	

Table 1: Estimates of effect of column species on abundance of row species. Significant effects are colored green for a positive relationship and red for a negative relationship. Species-pairs falling in the same habitat group are colored in a darker green or red than pairs of species in different habitat groups. Significance was determined at the 95% confidence level.

Species' abundances were largely negatively correlated, with the exception of some primarily pelagic species. Species with the highest number of significant relationships with other species were the blue shark (12), pelagic thresher (*Alopias pelagicus*; 11), spot-tail shark (*C. sorrah*; 11), and tiger shark (11). The silvertip shark and crocodile shark (*Pseudocarcharias kamoharai*) were affected by the abundances of the highest number of other species, at 16 each.

Interspecific interactions review

Table 3 shows the results of the diet literature review for the Indian Ocean, while Table 4 shows predation between study species in all oceans. Metadata tables with references are included in

PREDATOR \ PREY	Bigeye thresher	Blue shark	Bull shark	Crocodile shark	Dusky shark	Great hammerhead	Longfin mako	Oceanic whitetip	Pelagic thresher	Por beagle	Sandbar shark	Scalloped hammerhead	Shortfin mako	Silky shark	Silvertip shark	Smooth hammerhead	Spinner shark	Spot-tail shark	Tiger shark
Bigeye thresher																			
Blue shark																			
Bull shark					1							1	1			1	1		
Crocodile shark																			
Dusky shark					1						1	1				1	1		
Great hammerhead					1													1	
Longfin mako																			
Oceanic whitetip																			
Pelagic thresher																			
Por beagle																			
Sandbar shark					1														
Scalloped hammerhead				1															
Shortfin mako					1							1				1	1		
Silky shark																			
Silvertip shark																			
Smooth hammerhead																			
Spinner shark					1														
Spot-tail shark																			
Tiger shark					1	1						1	1				1		

Table 2: Predation relationships between study species in the Indian Ocean. A 1 represents that the column species has been found in the stomach contents of the row species.

the supplementary materials.

The shortfin mako, bull shark (*C. leucas*), and tiger shark have been recorded to consume many of the study species (Fig. 4). These species are also the only three that feed on sharks from two other habitat groups. The bull shark significantly increased in abundance during the USSR survey, while the tiger shark and shortfin mako decreased. The dusky shark was eaten by the most study species.

PREDATOR		Bigeye thresher	Blue shark	Bull shark	Crocodile shark	Dusky shark	Great hammerhead	Longfin mako	Oceanic whitetip	Pelagic thresher	Porbeagle	Sandbar shark	Scalloped hammerhead	Shortfin mako	Silky shark	Silvertip shark	Smooth hammerhead	Spinner shark	Spottail shark	Tiger shark
	Bigeye thresher																			
	Blue shark		1								1									
	Bull shark			1		1							1	1			1	1		
	Crocodile shark																			
	Dusky shark					1						1	1				1	1		
	Great hammerhead					1													1	
	Longfin mako																			
	Oceanic whitetip																			
	Pelagic thresher																			
	Porbeagle																			
	Sandbar shark					1						1								
	Scalloped hammerhead				1															
	Shortfin mako		1		1	1					1		1	1			1	1		
	Silky shark																			
	Silvertip shark																			
	Smooth hammerhead																			
	Spinner shark					1														
	Spottail shark																			
	Tiger shark					1	1					1	1	1				1		1

Table 3: Predation relationships between study species in all oceans. A 1 represents that the column species has been found in the stomach contents of the row species.
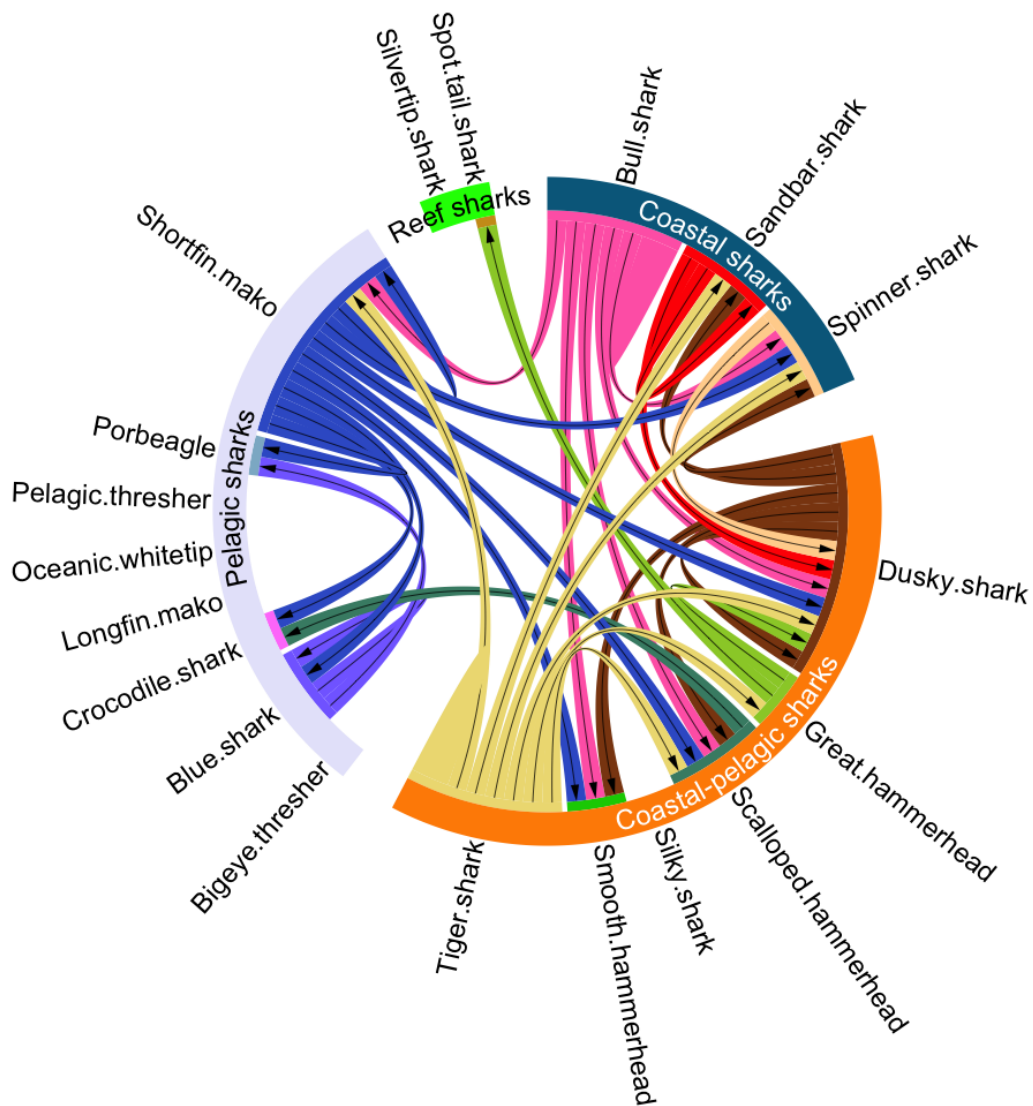
Fig. 4. Predation relationships between study species resulting from a literature review of their stomach contents in all oceans. Arrows are directed from predator toward the prey.

From the studies identified in the literature review, we recorded the percent by mass of sharks in the stomach contents of our study species, and calculated a weighted average between studies. From studies conducted in the Indian Ocean, we found sharks to be over half of the shortfin mako's diet by mass (54.1%, n=411 stomachs, N=3 studies). Including studies from outside the Indian Ocean, though, decreased the proportion of sharks in the shortfin mako's diet

to 17.0% (n=1447, N=14). Other species for whom sharks were a significant portion of their diet were the great hammerhead (*Sphyrna mokarran*; 46.8%, n=77, N=1), dusky shark (30.8%, n=757, N=2), tiger shark (25.0%, n=808, N=2), and bull shark (19.1%, n=464, N=3).

Several species were relatively isolated trophically, neither eating nor being eaten by other study species in any ocean. These were the bigeye thresher (*A. superciliosus*), longfin mako (*Isurus paucus*), oceanic whitetip, pelagic thresher, silky shark, silvertip shark, and spot-tail shark. To gather information on other ecological relationships, we also performed a literature review of competition between study species (Table 4).

The literature on competitive relationships between sharks was fairly scarce. We found that the silky shark had the most competitive relationships, with the blue shark, oceanic whitetip, and smooth hammerhead (*S. zygaena*). Other competitive pairs were the dusky shark and scalloped hammerhead (*S. lewini*), and sandbar shark and spinner shark (*C. brevipinna*). In all of these pairs except silky shark-smooth hammerhead and dusky shark-scalloped hammerhead, one species significantly declined during the USSR survey while the other significantly increased.

Trends in community composition

We compared relative abundances of sharks in different habitats throughout the Indian Ocean at the beginning and end of the USSR survey. To model on such a large spatial scale, we categorized the species from the USSR survey into four groups based on their habitat preferences: reef residents, coastal sharks, open ocean (pelagic) sharks, and sharks that inhabit both the open ocean and coasts (coastal-pelagic). We divided neritic (shallow water) habitats into continental and seamount habitats and open ocean (deep water) habitats into epipelagic and mesopelagic zones. Across all latitudes in the Indian Ocean, the rise in coastal-pelagic species from 1966 through 1989 was most pronounced in neritic habitats (Fig. 5A, D). The increase in reef sharks

	Bigeye thresher	Blue shark	Bull shark	Crocodile shark	Dusky shark	Great hammerhead	Longfin mako	Oceanic whitetip	Pelagic thresher	Porbeagle	Sandbar shark	Scalloped hammerhead	Shortfin mako	Silky shark	Silvertip shark	Smooth hammerhead	Spinner shark	Spottail shark	Tiger shark
Bigeye thresher																			
Blue shark														-1					
Bull shark						*													*
Crocodile shark																			
Dusky shark												-1							
Great hammerhead			*																*
Longfin mako																			
Oceanic whitetip														-1					
Pelagic thresher																			
Porbeagle																			
Sandbar shark																		-1	
Scalloped hammerhead					-1														
Shortfin mako																			
Silky shark		-1						-1								-1			
Silvertip shark																			
Smooth hammerhead														-1					
Spinner shark											-1								
Spottail shark																			
Tiger shark			*			*													

Table 4: Competition noted between species in the literature on all oceans in a symmetric matrix, noted by a -1. ∗ OShea et al. (2015) noted an event in which a bull shark, tiger shark, great hammerhead, and Caribbean reef shark (*C. perezi*) competed for a Caribbean reef shark caught on a longline, but do not draw conclusions due to the human influence in creating the situation.

allowed them to maintain similar proportions in neritic communities at the start and end of the USSR survey (Fig. 5A, D). While coastal species stayed relatively stable in true abundance, they declined in relative abundance in neritic communities, especially those close to landmasses (Fig. 5A, D). Pelagic species declined in relative abundance across all habitats.
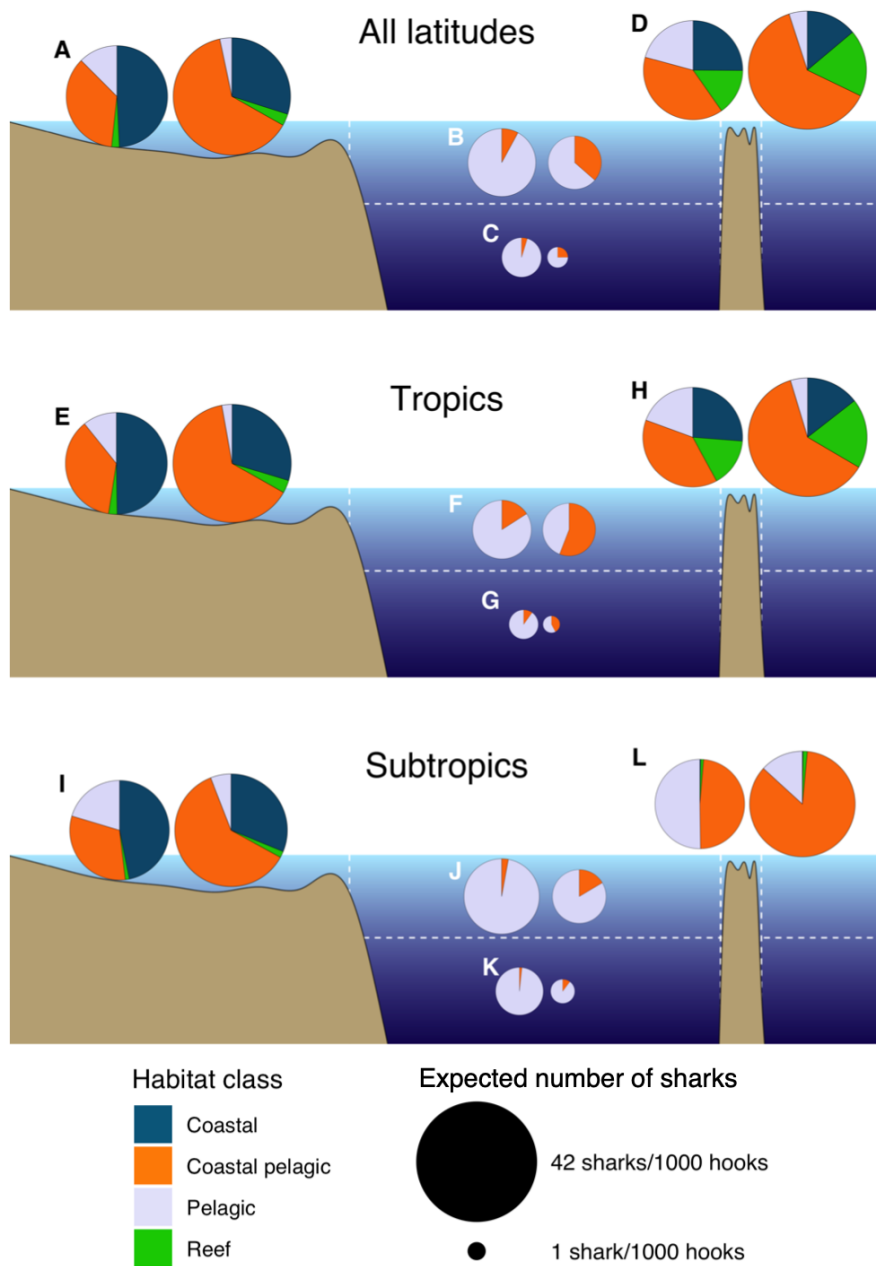
Fig. 5. Relative abundances of the four major habitat classes across all latitudes in the (A) nearshore neritic pelagic zone, (B) open-ocean epipelagic zone, (C) open-ocean mesopelagic zone, (D) offshore neritic pelagic zone; tropical (latitude between 23.5°N and 23.5°S) (E) neritic pelagic, (F) open-ocean epipelagic, (G) open-ocean mesopelagic, (H) offshore neritic pelagic; subtropical (latitude greater than 23.5°N and 23.5°S) (I) nearshore neritic pelagic, (J) open-ocean epipelagic, (K) open-ocean mesopelagic, and (L) offshore neritic pelagic zone. Pie charts on the left represent abundances in 1966, and on the right in 1989. Sizes of pie charts are proportional to the log of the sum of the predicted number of sharks.

The relative increase of coastal-pelagic sharks in the open ocean was most prominent in the tropics, where they grew from a minority at the beginning of the USSR survey to over half of the epipelagic open ocean community in 1989 (Fig. 5F). This growth nearly offset the overall decrease in sharks in the tropical epipelagic, but did not have as much of a compensatory effect in the mesopelagic. In the subtropics, the open ocean remained dominated by pelagic sharks, though the lower growth of coastal-pelagic sharks meant a larger decrease in abundance of sharks overall (Fig. 5J, K). In shallower waters, coastal-pelagic sharks grew to dominate both subtropical nearshore and offshore neritic habitats (Fig. 5L). Despite the rise in coastal-pelagic sharks, the total abundance of both the epipelagic and mesopelagic open ocean communities declined over the USSR survey period across all latitudes. The mesopelagic community was particularly affected.

Discussion

A USSR survey that spanned 24 years showed that initially species' trajectories were variable, experiencing both significant upwards and downwards trends at the onset of industrial fishing. Species vulnerability to exploitation did not adequately explain these trends, which instead were correlated among large ecotypes and suggested a prevalent role of interspecific interactions. Modeling abundances found the species to be highly dependent on each other. A literature review confirmed that the study species are known to prey on and compete with each other, though literature is limited on competition between sharks in any ocean. Strictly pelagic shark

species declined while coastal-pelagic sharks increased significantly, though this increase was not enough to offset an overall decline in abundance in open ocean shark communities. Our results indicate that fishing has altered these open ocean shark communities, diminishing species interactions and eroding the ecological roles played by sharks.

The historical USSR survey logged a large diversity of species that enabled us to observe how species respond to fishing in a way that has not previously been possible. We considered a variety of factors encompassing life history traits (as a proxy for biological vulnerability) and exposure to industrial fishing that could have contributed to the differential responses to fishing we found in the data. None of these variables or combinations thereof were able to sufficiently explain the responses across species. Absent inter-species interactions, the introduction of fishing pressure would also not change a species' life history traits in a way that would increase its abundance.

From the lack of significance of life history and vulnerability and the increase in abundance of some species, we conclude that interactions between species came into play as a driver of community change (Baum & Worm, 2009; Ferretti et al., 2010). The role of inter-specific dynamics in how sharks respond to disturbance has previously been hypothesized in modeling studies (Kitchell, Essington, Boggs, Schindler, & Walters, 2002). Release from predation on smaller shark species by the decline of larger sharks has been hypothesized to explain trophic cascades observed off the coast of South Africa and Eastern USA (Ferretti et al., 2010). Similarly, releases from predation and competition have frequently been suggested to explain changes in elasmobranch communities impacted by multispecies fisheries (Dulvy & Reynolds, 2002). The decline of large species known to eat other sharks, such as the great hammerhead, shortfin mako, and tiger shark, may have reduced the natural mortality of other sharks (Groeneveld et al., 2014a; Dicken et al., 2017a; Raoult, Broadhurst, Peddemors, Williamson, & Gaston, 2019), increasing the survivorship of smaller species and juveniles of larger sharks

(Ferretti, Curnick, Liu, Romanov, & Block, 2018). We also find that indirect relationships can play a role, as we hypothesize that the silky shark was likely minimally affected by changing predator abundances, and more likely was influenced by the decline of species known to compete with it in the Indian Ocean (Rabehagasoa et al., 2012). However, it is important to note that the absence of silky sharks in stomach contents could be due to sampling bias or difficulties in classification, and is not proof that silky sharks are never eaten by other sharks.

With increasing conservation attention on sharks, we hypothesize that competition and predation will again play a role in how species rebound. We have documented significant changes in the community composition of sharks in the Indian Ocean. These changes can result in new dynamics, such as increased competition and predation for juvenile apex predators from adults of a lower trophic level species (Baum & Worm, 2009). Current shark conservation and management efforts tend to have either a single species approach (Young & Carlson, 2020; Shiffman & Hammerschlag, 2016) or treat the group as a single species (Boyse, Goodman, & Beger, 2023; Griffiths et al., 2010; Hinke et al., 2004; Choy, Wabnitz, Weijerman, Woodworth-Jefcoats, & Polovina, 2016), but our findings suggest that changes in abundances do not occur independently of each other, and these interactions can produce unexpected results. We emphasize that successful ecosystem-based management must include all sharks at the species level to fully capture the dynamics within an ecosystem.

This study depended on standardized catch rates, which can be affected by species targeting and the resulting changes in fishing tactics between fleets (Winker, Kerwath, & Attwood, 2014). Within the USSR data, we do not expect these factors to have influenced catch rates, as the researchers conducting the survey were not targeting a particular species, and the same longline gear was used throughout the study period (Romanov et al., 2006).

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Supplementary Text

Variables used to explain variation in abundance changes

We regressed the IRCs of the 19 species caught in the USSR survey against seven variables, none of which had a statistically significant relationship with the IRCs.

Rmax

Rmax is the maximum growth potential of a species and thus an indicator of how it may respond to increased mortality. Where Indian Ocean-specific life history information was available, either in FishBase (Boettiger et al., 2012) or in the IOTC stock assessments, we used this information. For all other information, we first used the mean value for the species in FishBase. If this value was not available, we searched the literature for an estimate. Table S85 shows the life history values used and the Rmax value, as well as references for data not obtained through FishBase. We used Then *et al.*'s (2015) for calculating mortality (M) from lifespan (Then, Hoenig, Hall, Hewitt, & editor: Ernesto Jardim, 2015):

$$M = 4.899 * lifespan^{-0.916} \tag{1}$$

We calculated Rmax using method 4 from (Cortés, 2016), where t_{max} is lifespan, t_{mat} is age at maturity, M is mortality, and fec is fecundity:

$$l_{alpha} = \frac{(1 - exp(-(1.5M)))}{(fec \times (1 - exp - (1.5M(t_{max} - t_{mat} + 1))))} \tag{2}$$

$$1 - exp(-(M + r)) - l_{alpha} \times fec \times 1.25 \times exp(-r \times t_{mat}) \times$$
$$(1 - exp(-(M + r)(t_{max} - t_{mat} + 1))) = 0 \tag{3}$$

$Rmax = 2r$, where r is the root to the above equations.

Lambda

As part of their ecological risk assessment, Murua *et al.* calculated the population finite growth rate, lambda, for 15 of the 20 species recorded in the USSR survey (Murua et al., 2018). These species were, in order of increasing lambda value, the pelagic thresher, crocodile shark, bigeye thresher, sandbar shark, dusky shark, longfin mako, porbeagle, silky shark, scalloped hammerhead, oceanic whitetip, shortfin mako, tiger shark, great hammerhead, smooth hammerhead, and blue shark.

Lmax

We used the maximum total length for each species from rfishbase (Boettiger et al., 2012), except where Indian Ocean-specific data were available from the species' IOTC stock assessments, with the hypothesis that larger sharks may have been more affected over the USSR survey period.

Trend in size

See section on regression of USSR size data.

Longline availability

Murua *et al.* calculated a similar metric to our hook concentration to quantify the horizontal spatial overlap between IOTC fishing effort and species habitat in the Indian Ocean (Murua et al., 2018). Longline availability is the percentage of the species' habitat that is fished. Murua *et al.* calculated this for 13 of the 19 species recorded in the USSR survey: pelagic thresher, crocodile shark, bigeye thresher, longfin mako, porbeagle, silky shark, scalloped hammerhead, oceanic whitetip, shortfin mako, tiger shark, great hammerhead, smooth hammerhead, and blue shark (Murua et al., 2018). We first considered only the susceptibility to longlines because of its predominance over other gear types in the Indian Ocean.

Longline susceptibility

In the ecological risk assessment performed by Murua *et al.*, susceptibility is defined by four terms: the horizontal spatial overlap (availability), the depth overlap with a species' range (encounterability), the probability that an individual of a species is captured given that the gear encounters it (selectivity), and post-capture mortality (Murua et al., 2018).

Susceptibility to longlines, purse seines, and gillnets

Murua *et al.* also calculated susceptibility of the 13 species to purse seines and gillnets (Murua et al., 2018). For each species, we calculated the average of its susceptibility to all three gear types.

Hook concentration

Using the IUCN-defined habitats for each species (IUCN, 2020) and the IOTC's effort data (Commission, 2021), we calculated the two-dimensional concentration of hooks in each species' habitat from the first year in the IOTC data, 1952, and the end of the USSR survey, 1989. We clipped each species' habitat shapefile to the IOTC's area of competence, determined the number of hooks within the polygon, and divided it by clipped polygon's area.

Trophic level

We used the trophic level from rfishbase (Boettiger et al., 2012) for each species, with the hypothesis that higher-trophic-level sharks may have been more affected by fishing.

PREY

PREDATOR	Bigeye thresher	Blue shark	Bull shark	Crocodile shark	Dusky shark	Great hammerhead	Longfin mako	Oceanic whitetip	Pelagic thresher	Por beagle	Sandbar shark	Scalloped hammerhead	Short fin mako	Silky shark	Silver tip shark	Smooth hammerhead	Spinner shark	Spot-tail shark	Tiger shark
Bigeye thresher																			
Blue shark																			
Bull shark					(Cliff & Dudley, 1991)							(Cliff & Dudley, 1991)	(Cliff & Dudley, 1991)			(Cliff & Dudley, 1991)	(Cliff & Dudley, 1991)		
Crocodile shark																			
Dusky shark					(Dudley, Cliff, Zungu, & Smale, 2005)						(Dudley et al., 2005)	(Dudley et al., 2005)				(Dudley et al., 2005)	(Dudley et al., 2005)		
Great hammerhead					(Cliff, 1995)													(Stevens & Lyle, 1989)	
Longfin mako																			
Oceanic whitetip																			
Pelagic thresher																			
Por beagle																			
Sandbar shark					Porter et al., unpublished data														
Scalloped hammerhead				(de Bruyn, Dudley, Cliff, & Smale, 2005)															
Shortfin mako					(Greeneveld et al., 2014b)							(Cliff, Dudley, & Davis, 1990)				(Greeneveld et al., 2014b)	(Greeneveld et al., 2014b)		
Silky shark																			
Silver tip shark																			
Smooth hammerhead					(Allen & Cliff, 2000)														
Spinner shark																			
Spot-tail shark																			
Tiger shark					(Dicken et al., 2017b)	(Dicken et al., 2017b)						(Dicken et al., 2017b)	(Dicken et al., 2017b)				(Dicken et al., 2017b)		

Table 5: Citations for predation relationships between study species in the Indian Ocean.

PREDATOR \ PREY	Bigeye thresher	Blue shark	Bull shark	Crocodile shark	Dusky shark	Great hammerhead	Longfin mako	Oceanic whitetip	Pelagic thresher	Porbeagle	Sandbar shark	Scalloped hammerhead	Shortfin mako	Silky shark	Silvertip shark	Smooth hammerhead	Spinner shark	Spot-tail shark	Tiger shark
Bigeye thresher		(Lopez, Melendez, & Barria, 2010; Hernández-Aguilar, Escobar-Sánchez, Galván-Magaña, & Abitia-Cárdenas, 2016)								(Lopez et al., 2010)									
Blue shark			(Boettiger et al., 2012)		(Cliff & Dudley, 1991)							(Cliff & Dudley, 1991)	(Cliff & Dudley, 1991)			(Cliff & Dudley, 1991)	(Cliff & Dudley, 1991)		
Bull shark																			
Crocodile shark																			
Dusky shark					(Dudley et al., 2005)							(Dudley et al., 2005)				(Dudley et al., 2005)	(Dudley et al., 2005)		
Great hammerhead					(Cliff, 1995)														
Longfin mako																		(Stevens & Lyle, 1989)	
Oceanic whitetip																			
Pelagic thresher																			
Porbeagle																			
Sandbar shark				(de Bruyn et al., 2005)	Potter et al., unpublished data						(Ellis & Musick, 2007)								
Scalloped hammerhead																			
Shortfin mako		(Wood, Wetherbee, Jaanes, Kohler, & Wilga, 2009; Preti et al., 2012; Stillwell & Kohler, 1982)	(Lopez, Melendez, & Barria, 2009)	(Groenevald et al., 2014b)	(Groenevald et al., 2014b)					(Lopez et al., 2009)		(Cliff et al., 1990)	(Lopez et al., 2009)			(Groenevald et al., 2014b)	(Groenevald et al., 2014b)		
Silky shark																			
Silvertip shark																			
Smooth hammerhead																			
Spinner shark					(Allen & Cliff, 2000)														
Spot-tail shark																			
Tiger shark					(Dicken et al., 2017b)	(Dicken et al., 2017b)					(Papastamatiou, Wetherbee, Lowe, & Crow, 2006)	(Dicken et al., 2017b)	(Dicken et al., 2017b)			(Dicken et al., 2017b)	(Dicken et al., 2017b)		(Boettiger et al., 2012)

Table 6: Citations for predation relationships between study species in all oceans.

	Bigeye thresher	Blue shark	Bull shark	Croco dile shark	Dusky shark	Great hammer head	Long fin mako	Oceanic whitetip	Pelagic thresher	Por beagle	Sand bar shark	Scall oped hammer head	Short fin mako	Silky shark	Silver tip shark	Smooth hammer head	Spinner shark	Spot-tail shark	Tiger shark
Bigeye thresher																			
Blue shark														(Rabehagasoa et al., 2012)					
Bull shark					(O'Shea, Mandelman, Talwar, & Brooks, 2015)														(O'Shea et al., 2015)
Croco dile shark																			
Dusky shark												(Bornatowski, Braga, Abilhoa, & Corrêa, 2014)							
Great hammer head		(O'Shea et al., 2015)																	(O'Shea et al., 2015)
Longfin mako																			
Oceanic whitetip														(Compagno, 1984)					
Pelagic thresher																			
Por beagle																			
Sandbar shark																	(CAPAPÉ et al., 2003)		
Scall oped hammer head					(Bornatowski et al., 2014)														
Shortfin mako																			
Silky shark		(Rabehagasoa et al., 2012)						(Compagno, 1984)								(Xu, Pethybridge, & Li, 2022)			
Silver tip shark																			
Smooth hammer head														(Xu et al., 2022)					
Spinner shark								(CAPAPÉ et al., 2003)											
Spot-tail shark																			
Tiger shark		(O'Shea et al., 2015)			(O'Shea et al., 2015)														

Table 7: Citations for competition between species.

Literature review citations

Figure 6 models

Classification of species by habitat

We defined four major types of sharks by habitat use: reef residents, coastal sharks, coastal-pelagics, and pelagic sharks. We assigned each species identified in the USSR survey to one of these categories using the "DemersPelag" and "Brack" fields from the "species" function from the rfishbase package (Boettiger et al., 2012) and "rl_habitat" function from the rredlist package (Chamberlain, 2018). The definitions for each habitat classification are:

- Reef resident:

  – DemersPelag = reef-associated, Brack = 0, and no open ocean habitats habitat listed by rl_habitat (e.x., silvertip shark)

- Coastal:

  – DemersPelag = reef-associated, Brack = 1, and neritic pelagic habitats listed by rl_habitat, but no open ocean habitat (e.x., blacktip shark)

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- – DemersPelag = benthopelagic and no open ocean habitats listed by rl_habitat (e.x., sandbar shark)

- coastal-pelagic:

  - – DemersPelag = reef-associated and open ocean habitats listed by rl_habitat (e.x., silky shark)

  - – DemersPelag = benthopelagic and open ocean habitats listed by rl_habitat (e.x., tiger shark)

  - – DemersPelagic = pelagic-oceanic and resident in non-open ocean habitats listed by rl_habitat (e.x., scalloped hammerhead)

- Pelagic:

  - – DemersPelagic = pelagic-oceanic and not resident in non-open ocean/neritic pelagic habitats listed by rl_habitat (e.x., blue shark)

Table S137 shows the classification for each species identified in the USSR survey using this scheme.

Modeling

To generate the relative abundances in Figure 6 in the main text, we generated a ZINB GAM for each of the four habitat classes. In addition to the explanatory variables used for modeling individual species, we added two more factor variables: one differentiating between seamounts and coastal habitat (pr_h), and the other differentiating between the Eastern and Western Indian Ocean (eastwest). Pr_h defines areas shallower than 200 m and within 100 nautical miles of shore as coastal habitat, shallower than 200 m and farther than 100 NM from shore as seamount habitat, and deeper than 200 m as open ocean. The eastwest variable is divided at the 75.5° line,

which was determined via a hierarchical cluster of the USSR data to determine how effort was distributed longitudinally. Because we wanted to predict values over a large spatial area, we also included a lat:lon interaction term. We used the same call for all classes to achieve uniform predictions. The model call for these species used all 14 explanatory variables in the dataset:

$$zinbgam(count \sim year + cos(month) + sin(month) + lat + lon + lat : lon+$$

$$soaktime + depth + coastdistance + basketlength + maxhookdepth + minhookdepth+$$

$$pr\_h + eastwest + offset(log(nhooks)),$$

$$count \sim year + cos(month) + sin(month) + lat + lon + lat : lon + soaktime+$$

$$depth + coastdistance + basketlength + maxhookdepth + minhookdepth + pr\_h+$$

$$eastwest + offset(log(nhooks)))$$

$$(4)$$

Where the first formula is the formula for the count process and the second is the formula for the zero process. The residuals for these models are shown in Figures S101-S104. The models are summarised in Tables S138-S141.

Table S85. Rmax values, life history values used to calculate Rmax, and associated references.

FAO code	Scientific name	Litter size	Reproductive cycle length	Lifespan	Age at maturity	Rmax	Additional references
pth	Alopias pelagicus	2.00	1.0	29	9.650000	0.0863	(IOTC, 2016b)
bth	Alopias superciliosus	3.00	1.0	25	10.500000	0.0822	(IOTC, 2016a)
als	Carcharhinus albimarginatus	5.50	2.0	31	12.650000	0.0690	(W. T. White, Last, Stevens, Yearsly, et al., 2006; Smart et al., 2017)
ccb	Carcharhinus brevipinna	10.50	0.5	20	5.500000	0.1401	(Fowler et al., 2005)
fal	Carcharhinus falciformis	11.50	2.0	25	14.000000	0.0635	(IOTC, 2016e)
cce	Carcharhinus leucas	9.25	2.0	32	11.616667	0.0736	NA
ccl	Carcharhinus limbatus	5.50	2.0	12	5.166667	0.1549	NA
ocs	Carcharhinus longimanus	8.00	0.5	22	5.500000	0.1375	(IOTC, 2017b)
dus	Carcharhinus obscurus	8.50	2.0	40	19.600000	0.0466	NA
ccp	Carcharhinus plumbeus	8.00	2.0	34	15.000000	0.0594	NA
ccq	Carcharhinus sorrah	4.50	1.0	8	2.400000	0.2931	(Harry, Tobin, & Simpfendorfer, 2013)
tig	Galeocerdo cuvier	46.00	2.0	50	6.500000	0.0968	NA
bsh	Prionace glauca	69.50	1.0	23	4.500000	0.1562	(IOTC, 2017a)
sma	Isurus oxyrinchus	10.00	3.0	32	15.000000	0.0596	(IOTC, 2016d)
lma	Isurus paucus	2.00	3.0	32	15.000000	0.0596	(Gilmore, 1993)
por	Lamna nasus	3.25	1.0	30	11.916667	0.0728	NA
spl	Sphyrna lewini	23.00	1.0	30	12.500000	0.0700	(IOTC, 2016c)
spk	Sphyrna mokarran	27.50	2.0	39	11.100000	0.0736	(Piercy, Carlson, & Passerotti, 2010; Harry, 2011; Cortés et al., 2015)
spz	Sphyrna zygaena	33.00	1.0	18	9.000000	0.0951	(Cortés et al., 2015)
psk	Pseudocarcharias kamoharai	4.00	2.0	11	4.100000	0.1883	(Oliveira et al., 2010; Lessa, Andrade, De Lima, & Santana, 2016)