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Preliminary analysis of crocodile shark (*Pseudocarcharias kamoharai)* distribution and abundance trends in pelagic longline fisheries

by

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ABSTRACT

Crocodile shark (*Pseudocarcharias kamoharai*) has a broad distribution across the world's oceans, but is a rare catch in most commercial fisheries. In some geographic areas, crocodile shark is an abundant bycatch of pelagic longline fisheries. Limited crocodile shark biological and fishery information is available to date. We analyzed worldwide pelagic longline fishery observer and research cruise survey data (1950-2005) to estimate crocodile shark abundance and distribution. Preliminary results suggested the highest crocodile shark catch rates were in the Indian Ocean. Off western Australia, crocodile sharks were one of the most frequently caught species. Results showed that in addition to ocean basin, target species, moon phase, season, bottom depth, gear fishing depth and deployment time significantly affected crocodile shark catches. In each fishery, encounters and catch rates increased with the number of years since exploitation commenced. Pelagic longline fisheries exploited the entire crocodile shark size range, with the species fully selected above 100 cm fork length and most crocodile shark were longer than the reported size at first maturity. The analysis revealed that the crocodile shark sex ratio varied among pelagic fisheries. Japanese Pacific yellowfin and US Pacific tuna fisheries captured more males, whereas US Atlantic swordfish and Japanese southern bluefin fisheries captured more females.

Keywords: crocodile shark, *Pseudocarcharias kamoharai*, longline fishing, rare species, abundance trends, geographical distribution

INTRODUCTION

There is great concern about the bycatch of open-ocean sharks in commercial fisheries because they mature late, have long life spans and low reproduction potential rendering them vulnerable to overexploitation (Dulvy et al., 2008). Crocodile shark (*Pseudocarcharias kamoharai*) is a small lamnoid shark that inhabits offshore waters of the world's oceans. Although the species is an abundant shark taken in some pelagic longline fisheries, limited biological and catch data is available. The lack of information is attributed to its low commercial value and relatively rare encounters in commercial fisheries during the last century. In most fisheries, crocodile sharks catches are rare; however, the species is frequently taken by pelagic longline gears (Compagno 2001; FAO 2008). Commercial fishers do not target or harvest crocodile shark despite the liver being large and rich in squalene (Abe, 1969). Crocodile sharks are discarded at sea because of their smaller size and lower market value in comparison to target and non-target (i.e., bycatch) pelagic longline species (Compagno 1984, 2001; FAO 2008).

Historically, crocodile shark were considered a rare and uncommon species during last century (D'Aubrey 1964; Krefft 1980; Cadenat and Blache 1981; Fujita 1981; Compagno 1982, 1984; Romanov and Zamorov 1994; Amorim et al. 1998). Today, numerous pelagic longline fishery studies, at least for some areas (Williams 1998; Ward et al. 2004; Molony 2005; Ward and Myers 2005a; Hender et al. 2007; Ariz et al. 2007; Basson et al. 2007; Oliveira et al. 2008), indicate that the species is frequently taken, which may reflect better reporting or subtle changes in longlining gear and fishing practices or population abundance is increasing.

Based on their life-history characteristics, the International Union for Conservation of Nature (IUCN) Red List of Threatened Species has listed crocodile shark as "Low Risk/Near Threatened" (Compagno and Musick 2000 in IUCN 2007a) or "Near Threatened" (IUCN, 2007b). However, ecological risk assessments in Australia's Eastern and Western Tuna and Billfish Fisheries classified crocodile shark as "medium risk" (Webb et al. 2008). Despite having limited information, the IUCN risk assessments suggest crocodile shark have declined significantly because of pelagic longline fisheries (Compagno and Musick 2000 in IUCN 2007a). However, no worldwide study of this species occurrence, distribution and trend in abundance has been available until now.

In this study, we summarise the available scientific literature on the biology, ecology, and distribution of crocodile shark, with particular attention to the Indian Ocean. We also examine worldwide data collected by pelagic longline research surveys and fishery observers aboard commercial pelagic longline fishing vessels to evaluate trends in global crocodile shark catches and estimate spatial variability in crocodile shark distribution.

REVIEW OF BIOLOGY AND ECOLOGY

The Lamniformes order consists of 7 families and 16 species. Of these, crocodile shark is the smallest (36-131 cm TL) and only species in the family Pseudocarchariidae. The species has a slender, spindle-shaped body and its eyes are large and lack nictitating eyelids (Compagno 2001). The dorsal surface is dark brown and fades to a whitish ventral surface (Fig. 1). Crocodile shark are distinguished from other mackerel sharks (i.e., Lamniformes) by their small size and prominent large eyes. They are sometimes confused with other shark species caught on pelagic longlines, such as dogfish (Squalidae) and sand tiger (Odontaspididae) sharks, especially bigeye sand tiger shark (*Odontaspis noronhai*) (Fig. 2).

Available information indicates crocodile shark are found in offshore waters of the Pacific, Atlantic and Indian Oceans (Table 1). They are an open-ocean species that are seldom found in shelf waters or shallow seas, such as the Mediterranean Sea and the Red Sea (Compagno 2001; Bonfil and Abdallah 2004; Serena 2005). Within the major oceans crocodile sharks are distributed between 44°S and 37°N, which roughly corresponds to the 20°C mean annual sea surface temperature isotherm (Gouretski and Koltermann 2004). Crocodile sharks have never been reported from higher latitudes, including the Indian Ocean (i.e., the waters off south-western Australia) or the western North Atlantic Ocean, despite considerable longline fishing effort in those areas.

Crocodile shark are distributed from near-surface waters to around 590 m. The species is considered mesopelagic, migrating from below the thermocline during the day and towards the surface at night (Last and Stevens 1994). The large, but non-reflective eyes, suggest nocturnal activity in the epipelagic zone, and possibly a diel movement pattern (Compagno 2001). Analyses of fine-scale data reported by fishery observers aboard commercial pelagic longline vessels operating in the central tropical Pacific Ocean indicate that crocodile sharks are uniformly distributed through the water column at night, but rarely taken in the upper mixed layer (<200 m) during the day (Ward and Myers 2005a).

Some information on crocodile shark reproduction is available. Compagno (2001) reported that the species are ovoviviparous, retaining the eggs, which hatch in the uterus. Several studies showed that females produce four pups (Abe 1973; Fujita 1981; White 2007) that are ophiphagous. Fujita (1981) and Compagno (2001) reported that the pups feed on ova and yolk sacs, which are produced by the mother. The size at birth is between 36 and 45 cm (Fujita 1981; White 2007). It is believed that reproduction takes place throughout the year since no seasonality in reproductive activity has been reported (Fujita 1981; White 2007; Oliveira et al. 2008). Males mature around 73 or 74 cm TL and females between 87 and 103 cm TL (Abe 1969; Fujita 1981; Compagno 2001; White 2007; Oliveira et al. 2008).

Limited information is available about crocodile shark feeding habits and its trophic position. The grasping dentition of crocodile shark suggests that they feed on small teleosts, cephalopods and crustaceans (Last and Stevens 1994). It was reported (Compagno 2001) that stomach contents include small bristlemouths (gonostomatids), lanternfish (myctophids), small shrimp, and squid beaks. Stomach contents may also include onychoteutids, mastigoteuthids, pholidoteuthids and cranchiids, but no detailed study of crocodile shark diet has been reported.

Knowledge of crocodile shark distribution and occurrence in catches is both limited and contradictory. In the Indian Ocean, crocodile shark was considered a rare species with uncertain distribution beyond Mozambique Channel (Compagno 1984; Fig. 3). Compagno (1984) indicated that crocodile shark was occasionally recorded in equatorial waters by Japanese, Korean and Chinese (Taiwan Province) pelagic longline fisheries. However, the few catches reported during 30-years of Soviet research longlining (Romanov and Zamorov 1994), suggests that crocodile shark are rare in equatorial waters, despite considerable spatial sampling coverage and fishing effort initiated in the area by the Soviet Indian Ocean Tuna Longline Research Program (SIOTLLRP)[1] (Fig.4). In contrast, crocodile shark appear to be one of the principal bycatch species in the western Australian swordfish pelagic longline fishery that developed in the late 1990s (Hender et al., 2007; Fig. 5). During 2004-05, crocodile shark were also reported as an abundant bycatch species of the Spanish experimental fishing program in the south-western Indian Ocean (Ariz et al. 2006; Fig. 5). The crocodile shark was the third and the tenth most frequently caught species in the Western Australian and Spanish fisheries, respectively. Such drastic variations in catch rates and, possibly, abundance during the past 10 to 15 years suggest potential changes in the population, its overall role in the open-ocean ecosystem or an increase of fishing effort within preferred crocodile shark habitats.

DATA AND METHODS

Pelagic longline catch and effort data collected by scientific fishery observers aboard commercial longline fishing vessels and during research surveys (1950-2005) (Table 1b) were analyzed to determine factors that influence distribution and catch rates of crocodile shark. In addition, data were evaluated to describe crocodile shark size and sex composition.

Fork length (FL), total length (TL), and sex were determined for each shark. We developed a morphometric relationship to convert length measurements using linear regression (where observers reported total length and fork length for the same crocodile shark). The length-length relationship was described by the following formula:

$$FL = 0.7516\,TL + 11.33 \;\; (n = 238;\ \mathrm{r}^2 = 0.8559;\ p < 0.0001) \qquad (1)$$

To evaluate and standardize changes in crocodile shark abundance represented in the reconciled data, we used generalized linear models (GLMs) to identify factors affecting crocodile shark catches. We chose to use GLMs because this approach accounts for data that are not necessarily normally distributed and the mean may not be a linear combination of parameters, but some function of the mean will be a linear combination of parameters (McCulloch and Searle 2001).

Preliminary results showed that the frequency distribution of catches was highly skewed, with many longline operations or “sets” having a zero or few (~ 1) crocodile shark catches (Fig. 8). Thus, to account for these low encounters, we used the delta-distribution approach to fit into the GLM framework, where crocodile shark presence-absence or “encounters” and catch levels were modelled separately (Barry and Welsh 2002; Maunder and Punt 2004). Catches were modelled using two steps. In step one (the encounter model), we obtained the probability of a non-zero catch by modelling crocodile shark encounters with a binomial error distribution and logit link using the following equation:

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[1] **S**oviet **I**ndian **O**cean **T**una **L**ongline **R**esearch **P**rogramme (SIOTLLRP), 1961-1989 research program of YugNIRO, Kerch, Ukraine under auspice of the Ministry of Fisheries of the USSR. For details see Romanov *et al.* (2006).

$$pa_i = \beta_0 + \beta_1 O_i + \beta_2 D_i + \beta_3 M_i + \beta_4 Q_i + \beta_5 Y_i + \beta_6 T_i + \beta_7 S_i + \beta_8 W_i) \quad (2)$$

where pa_i is the presence or absence of a crocodile shark, O_i is the effect of region (Pacific, Atlantic or Indian Ocean), D_i is the depth category (shallow, regular, or deep), M_i is the moon phase, Q_i is the three-month quarter, Y_i is the period of exploitation in the fishery (years), T_i is the time when longline deployment commenced (night or day), S_i is the target species and W_i is the category of water depth (<2000 m, 2000-4000 m, 4000-6000 m or >6000 m) of longline operation *i*. The $\hat{a}_j$ are estimated parameters.

In step two (the catch model), we modelled catches for those longline operations where at least one crocodile shark was caught using a truncated Poisson distribution using the following equation:

$$c_i = \beta_0 + \beta_1 O_i + \beta_2 D_i + \beta_3 Q_i + \beta_4 Y_i + \beta_5 S_i + \beta_6 W_i + \log(h_i) \quad (3)$$

where c_i is the number of crocodile shark that were caught in a longline operation. We included the offset term h_i for the total number of hooks deployed in the longline operation to account for the differing number of hooks set in each operation.

For these analyses, exploitation years were modelled as a continuous variable and all other variables were modelled as categorical variables. To standardize seasons and be able to compare among regions, operations in the southern hemisphere (i.e., the three-month quarter) was offset by six months so that they represented the same season as the northern hemisphere. Since the modelling aimed to identify variables that influenced crocodile shark distribution, we did not explore interactions among variables.

We implemented the models in *R* Language for Statistical Computing (R Development Core Team, 2006) using the GLM function in the MASS package. Model selection involved the stepwise removal of non-significant variables to identify a set of variables that significantly affected crocodile shark encounters (i.e., positive catches). We used a parametric bootstrap procedure to estimate uncertainty around the predicted catch rate. For each bootstrap sample, a presence–absence random variable was generated from a Bernoulli distribution and a catch variable was generated from a truncated Poisson distribution for each data record. To estimate the overall catch rate, we multiplied the two sets of predictions.

RESULTS

There were 30 678 longline operations (i.e., sets) with data for all the variables that we modelled. Of the total number of sets, 98% did not catch any crocodile sharks, while most of the remainder caught only one animal. The total number of crocodile sharks taken was 1685 individuals (Fig. 8). The number of crocodile sharks caught in one operation (i.e, set) ranged from 0 to 53. The largest catch of this species was reported by a fishery observer aboard a Japanese longline vessel operating off western Australia. Overall, the highest nominal catch rates of crocodile shark were in the Australian Indian Ocean swordfish (*Xiphias gladius*) and Japanese Indian Ocean yellowfin tuna (*Thunnus albacares*) fisheries (Table 1a).

Data showed pelagic longline fishery operations targeted tuna (87%) and swordfish (13%). The main target species were yellowfin, bigeye (*Thunnus obesus*), or southern bluefin tuna (*Thunnus maccoyii*), which involved longline deployment in the early morning. To target swordfish, fishermen usually deployed shallow longlines (<150 m) at night using squid as bait and artificial light sticks as attractants (Ward et al. 2000). Fishery characteristics showed pelagic longline operations were uniformly distributed with respect to season (three-month quarter) and moon phase (Fig. 8). Modelling showed that the species was rarely encountered by deep longline operations and the highest catch rate was for the Indian Ocean data (Table 2-3; Fig. 9). However, recent Spanish data was not available at the time of analysis, which may influence these conclusions. Overall, results revealed most crocodile sharks were taken by fishery operations targeting bigeye tuna, in the first quarter of the year and during the full moon. The number of crocodile shark encounters and catch rates increased with the number of years since pelagic longlining commenced in each fishery (Fig. 9). We found variables, such as calendar year, latitude, and longitude were highly correlated with other variables, but we did not find any significant affect on crocodile shark encounters or catch rates.

The catch model was generally consistent with the encounter model (Table 3); however, the catch model showed that in pelagic longline operations that caught one or more crocodile shark, catch rates were lower in the Pacific Ocean than in other oceans.

Depending on the fishery, catches of crocodile shark varied by sex. In the Japanese Pacific yellowfin ($p < 0.002$) and US Pacific tuna fisheries ($p < 0.001$), there were significantly more male crocodile shark, whereas there were significantly more females in US Atlantic swordfish ($p < 0.001$) and Japanese southern bluefin ($p < 0.004$) fisheries (Table 4). Overall, male crocodile shark outnumbered females ($p < 0.001$).

The crocodile shark length frequency distribution ranged from 39 to 185 cm FL (Fig. 7). Our results revealed that the smallest crocodile shark (39 cm) taken was within the size-at-birth range (36-45 cm) reported by various researchers (Fujita 1981; Heemstra 1995; White 2007). Most (68%) of the crocodile sharks taken in each pelagic longline fishery was longer than the reported length of maturity for males (72-74 cm FL) and females (> 87 cm FL) (Abe 1969; Fujita 1981; Compagno 2001; White 2007; Oliveira et al. 2008). In fact, the lengths of several crocodile shark reported by Australian fishery observers aboard Japanese longline vessels operating in the western Pacific and eastern Indian Ocean were much longer than the 110 cm maximum reported by Romanov and Zamorov (1994) or the recently reported animal (131 cm TL) (unpublished data, Sujittosakul and Sujittosakul 200X; Fig. 7). However, taking into consideration particular biological features of crocodile sharks (small size at birth, size at maturity, and documented cases of misidentification (Anon. 1999), all records of crocodile shark longer than 135 cm TL are doubtful and should be interpreted with caution.

Crocodile shark reproduction was not specifically evaluated for this study; however, Australian observers investigated several hundred mature female crocodile sharks. Dissections did not find any pups (Jay Hender, pers. comm.).

DISCUSSION

Geographical Distribution

Crocodile shark is broadly distributed between 44°S and 37°N (Fig. 6). However, their distribution is more heterogeneous than the distributions of highly migratory tuna, billfish, and other pelagic shark species, such as blue shark and oceanic whitetip shark (Last and Stevens 1994). Encounter rates and catch rates were highest in the Indian Ocean. These preliminary results suggest that crocodile shark is more abundant in the Indian Ocean than in the other basins. However, we believe the species displays a clumped distribution pattern rather than an even distribution, resulting in low encounter rates for other areas. At this time, it is difficult to explain our observations because of the challenges in separating the actual variations in the species' geographical availability, or abundance, from the effects of other factors on crocodile shark encounters, such as the different fishing gear and practices and temporal extent of fisheries. Also, low levels of fishing effort may have been responsible for the absence of crocodile shark in several broadly distributed surveys (Table 1b). Additional analyses are warranted. We therefore suggest that our results are preliminary and need to be interpreted with caution.

Overall, the crocodile shark appears to have a limited distribution. Crocodile shark is abundant in the tropical Pacific Ocean, but rare in the subtropics (Bailey et al. 1996, Molony 2005). We found that the opposite pattern occurred in the Indian Ocean where the species is abundant in the subtropics and rare in the tropics.

Historical trends

The models showed that crocodile shark abundance, as indexed by pelagic longline encounters and catch rates, has increased with years of fishing exploitation (Fig. 9). This trend suggest an example of predator release, where the "fishing down" of large predators, such as pelagic sharks and billfish, has resulted in the increase of abundance of smaller pelagic species, such as crocodile shark. However there are no records on predation for this species by any top predator to support our observations. The low occurrence and rarity of crocodile shark during last century may explain the absence of such records. However similar trends have been documented for other species. For example, Ward and Myers (2005b) suggested predator release as a possible explanation for the increase in abundance of pelagic stingray (*Pteroplatytrygon violacea*) in the Pacific longline fishery since longlining commenced in the early 1950s.

Nevertheless, the increase in abundance is not consistent with several life-history characteristics of crocodile shark (e.g., their moderate litter size and limited mobility), which make them vulnerable to overfishing. Coincidentally, those biological characteristics are similar to those of pelagic chondrichthyans, which Ward and Myers (2006) hypothesized had increased in abundance in response to the reduced abundance of large predators. For crocodile shark, an unbalanced sex ratio might increase their vulnerability to overexploitation by commercial fisheries. If crocodile shark is similar to blue shark (with 'male hotspots' and 'juveniles aggregations' (Litvinov 2006)) then it is plausible that excessive fishing effort in localized areas may negatively affect crocodile shark populations. The absence of pregnant females in the temperate waters around Australia (Jay Hender, pers. comm.) and the overall male dominance in subtropical-temperate waters (this study, Ariz et al. 2006, 2007) compared with prevalence of females and reproductive activities in tropical waters of

Indonesia (White 2007) suggest spatial or functional segregation of juveniles, males and females.

Our results showed that crocodile shark encounters and catch rates are increasing, but this might be the result of an artefact of the different data sets that we analysed. In general, commercial fisheries increase precision and catchability with time. Therefore, new and emerging fisheries with a shorter exploitation history will sometimes employ fishing gear, technology, or techniques that produce high encounters and catch rates than in previous years. By comparison, the gear or practices used in early years might have produced low encounters and catch rates. Another plausible explanation for the historical increase in catch rates is the long-term variations in crocodile shark encounters due to the fluctuations in broad-scale oceanographic shifts. We hypothesize that global variation in oceanographic conditions, such as the rising sea surface temperature and increasing heat content (Gouretski, Koltermann 2007), which influenced the position of thermocline depth, might affect the survival of pups, population productivity, and the distribution thereby increasing the vulnerability of crocodile shark to pelagic longline fisheries.

CONCLUSIONS

The distribution of crocodile shark is more fragmented and displays a clumped distributional pattern compared to highly migratory species, such as tunas, swordfish, and billfish. Although our modelling did not explain why crocodile shark are more frequently caught in some pelagic longline fisheries than others, our findings showed that crocodile shark encounters and catch rates increased over time. Additional, evaluations are necessary to explain whether this represents an increase in abundance due to predator release or is an artefact of the different data sets. More detailed information on the catchability of longline fishing gear, combined with information on crocodile shark biology and stock structure, will be required to understand their peculiar distribution and historical catch trends and, ultimately, estimate population status. Because the reasons why catches of crocodile shark are increasing is unknown and specific stock assessments are lacking, it is advisable that the cautionary approach be taken by international fishery management organizations so that these susceptible species do not become unnecessarily threatened by global pelagic longline fisheries.

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Table 1a. Summary of published information on crocodile shark distribution, abundance, biological parameters [a]

Area	Period	Gear[b]	Type of record[c]	Type of data collection[d]	Abundance[e]	No of individuals recorded	Size (mm)[f]			Sex ratio (M:F)	% of the cath		nominal CPUE		Reference
							M	F	Both / unident.		weight	number	hook rate (ind×1000 hooks^{-1})	catch rate (kg×100 hooks^{-1})	
Western Pacific (Japan ?)	1930s		N			1?									Matsubara 1936
Western Pacific (Taiwan)	1950s														Teng 1959, 1962
Equatorial Atlantic (Guinea)	1960s		N	SC	R	1	975								Cadenat 1963
South-western Indian Ocean	1960s		N	SC	R	1?									D'Aubrey 1964
Central Atlantic (12°07'N, 23°08'W)	1968	TRAW	N	SC	R	1		1020							Krefft 1980
South-western Indian Ocean	1970s														Bass *et al.* 1975
Central Pacific (11°26'-18°55'N, 161°35'-167°59'W)	1979	LL	R	SC		11	935	977-985		2.7:1					Fujita 1981
Eastern Pacific (8°52'S, 88°05'W)	1982	IKMT	R	SC	R	1			460						Kashkin 1989
South-western Atlantic off Brazil	1983-1988	LL	R	VC		73			3.21[g]			0.34	0.01-0.05		Hazin *et al.* 1990
Western Central Indian Ocean (0°55'N-5°11'S, 55°14-66°11E)	1984-1987	LL	N	SC	R	3	1024	1077-1100		1:2					Romanov, Zamorov 1994
Eastern Tropical Pacific, Baja California (25°40'N, 129°00'E)	1994	LL	N	SC	R	1		992							Long, Seigel 1996
South-western Atlantic off Brazil	1986-1991	LL	N+R	SC		56		850-1120		2.3:1					Amorim *et al.* 1998
Western Pacific	1978-1992	LL	R	O	R→C	>7									Bailey *et al.* 1996
Western Pacific	1994-1997	LL, PS	R	O	C	101				4.8:1		0.5	0.05-0.115	0.031[h]	Williams 1996, 1999
South-eastern Pacific, Peru (17°39'S, 71°21'W)	2000	LL	N	SC	R	1	830								Bearez *et al.* 2001
South-western Pacific , New Zealand (32°14'S, 172°16'E)	2000	LL	N	SC	R	1	1096								Stewart 2001

Area	Period	Gear[b]	Type of record[c]	Type of data collection[d]	Abundance[e]	No of individuals recorded	Size (mm)[f]			Sex ratio (M:F)	% of the cath		nominal CPUE		Reference
							M	F	Both / unident.		weight	number	hook rate (ind×1000 hooks^{-1})	catch rate (kg×100 hooks^{-1})	
Pacific Ocean	1950-2002	LL	R	O, SC	R→C	468							0.03		Ward & Myers 2005; Ward *et al.* 2004
South Atlantic (5N-15S)	1999-2003	LL	R	O		242						2.68	2.42	-	Joung *et al.* 2005
Western Pacific	1990-2004	LL	R	O	C	1799							~0.37-1.02		Molony 2005
Western Pacific, off Queensland, Australia	~2002-2003	LL	R	SC		1	870[i]				-				Lisney, Collin 2006
South-western Indian Ocean	1998-2005	LL	R	O	C								1.37		Petersen, Honig 2006
South-eastern Atlantic (Namibia, South Africa)	2000-2005	LL	R	O	R→C	91							0.0-0.2		Basson *et al.* 2007
South-eastern Pacific, Chile (22°06'S, 83°32'W)	2005	LL	N	SC	R	1		920							Melendez *et al.* 2006
South-western Indian Ocean	2005	LL	R	O	C	534	780-1180	79-1170		13.6:1	0.22				Ariz *et al.* 2006, 2007
Eastern Indian Ocean, Indonesia	2001-2006	LL ?*	R	SC	C	77	363-1068	434-1181		1:2.5					White 2007
Indian Ocean	2006	LL	R	O	C	24			68-89[j]	1:1.6		0.65	0.08		Okamoto *et al.* 2007
South-western Atlantic off Brazil	2005-2007	LL	R	SC	A	490	1090	1220		1:1.8					Oliveira *et al.* 2008
Eastern Indian Ocean	2001-2005	LL	R	SC	C	6			118-131[k]						Rajruchithong *et al.* 2005
Worldwide	1937-2000?				R→A										Compagno 1984, 2001

[a] Some references summarize same datasets, [b] LL-pelagic longline, TRAW-midwater trawl, IKMT-Isaacs-Kidd Midwater Trawl, *sampling at the landing sites, [c] N-new record, R-routine observations, [d] O-observers records, SC-scientific collection, VC-vessel crew, [e] R-rare, C-common, A-abundant, [f] TL if not specified otherwise. One value means maximum recorded length, [g] Mean weight, [h] for PS (kg×set^{-1}), [i] FL, [j] SL, [k] Size information is from Sujittosakul, Sujittosakul, 200X.

Table 1b. Summary of observer and survey longline data that we used to describe the distribution and composition of pelagic longline catches of crocodile shark. Datasets are listed in descending order of their nominal catch rates of crocodile shark.

Dataset name	Area	Period	Year commenced	Deployment time	Depth range (m)	Target species[a]	Operations (no.)	Hooks (hooks*10^6)[c]	Crocodile shark	
									(no.)	(cpue[b])
AU Indian swordfish	SE Indian	2003–05	1965	night	25–150	SWO	102	0.133	373	2.813
JP Indian yellowfin	SE Indian	1991–97	1965	day	30–200	YFT, BET	372	0.682	876	1.284
SIOTLLRP	Indian Ocean	1961-89	1960	day	25–400	YFT, BET, SHK	428	0.234	169	0.721
SU Pacific survey	E Pacific	1984	1961	day	65–230	YFT, BET	44	0.013	8	0.606
US Atlantic swordfish	W Atlantic	1992–2003	1956	night	–	SWO	2 415	1.348	157	0.116
US Pacific bigeye	central Pacific	1994–2002	1951	day	27–600	BET, YFT	5 607	10.451	369	0.035
AU Pacific swordfish	SW Pacific	2001–03	1961	night	–	SWO	33	0.031	1	0.033
US Pacific swordfish	NE Pacific	1994–2002	1989	night	–	SWO	2 459	1.993	61	0.031
JP southern bluefin	S oceans	1980–96	1965	day	–	SBT	2 513	5.105	91	0.018
SPC Pacific bigeye	W Pacific	1993–2001	1951	night	–	BET	7 102	6.750	101	0.015
JP Pacific yellowfin	SW Pacific	1982–96	1961	day	30–200	YFT, BET	1 624	3.712	55	0.015
SPC Pacific bigeye day	W Pacific	1990–2001	1951	day	–	BET, YFT	12 940	27.708	77	0.003
AU Pacific yellowfin	SW Pacific	2001–03	1961	day	25–300	YFT, BET	511	0.444	1	0.002
US Atlantic tuna	W Atlantic	1992–2003	1956	day	–	YFT, BET	3 396	2.618	5	0.002
NZ Pacific yellowfin	SW Pacific	1988–2004	1961	night	–	SBT	5 525	12.277	1	0.000
SU Atlantic survey	Atlantic	1978–86	1956	day	0–230	YFT, BET	245	0.064	0	0.000
UK Indian Ocean	Indian Ocean	1999–2004	1960	day	50–150	YFT, BET	63	0.135	0	0.000
UR Atlantic surveys	E Atlantic	1969–89	1956	day	50–350	YFT, BET	242	0.231	0	0.000
US Pacific survey	central Pacific	1950–58	1950	day	26–200	YFT	1 155	0.459	0	0.000
						Total	46 776	74.389	2 345	0.032

[a] Species codes: SWO – swordfish *Xiphias gladius*, BET – bigeye tuna *Thunnus obesus*, SBT – southern bluefin tuna *Thunnus maccoyii*, SHK – sharks, YFT - yellowfin tuna *Thunnus albacares*, TUN – tunas, MIX – mixed species

[b] Hook rate, i.e. number of crocodile shark per 1000 hooks

Table 2. Parameter estimates and statistics for the encounter model

Variable	Estimate	SE	z-value	*p*-value[a]	
(Intercept)	-0.3556	0.3885	-0.9150	0.3601	
Ocean (Atlantic)	-0.7390	0.2030	-3.6410	0.0003	***
Ocean (Indian)	0.6955	0.1866	3.7280	0.0002	***
Depth (deep)	-1.0150	0.1432	-7.0890	0.0000	***
Depth (regular)	-0.7346	0.1591	-4.6170	0.0000	***
Moon phase 1	0.2200	0.1111	1.9800	0.0477	*
Moon phase 3	-0.4124	0.1225	-3.3660	0.0008	***
Moon phase 4	0.1687	0.1101	1.5330	0.1254	
Quarter II	-0.5972	0.1211	-4.9300	0.0000	***
Quarter III	-0.2045	0.1127	-1.8140	0.0696	.
Quarter IV	-0.4302	0.1148	-3.7480	0.0002	***
Exploitation years	0.0234	0.0050	4.6310	0.0000	***
Deployment time	0.6140	0.1311	4.6830	0.0000	***
Target species (MIX)[b]	-3.1000	1.0250	-3.0240	0.0025	**
Target species (SHK)[b]	-2.6850	1.0110	-2.6550	0.0079	**
Target species (SWO)[b]	-0.4561	0.1668	-2.7340	0.0063	**
Target species (YFT)[b]	-0.7216	0.1255	-5.7520	0.0000	***
Water depth 1	-3.7010	0.2661	-13.9040	0.0000	***
Water depth 3	-1.4500	0.3403	-4.2600	0.0000	***
Water depth 4	-0.7230	0.3475	-2.0810	0.0375	*

[a] Statistical significance: *** <0.001
** 0.001–0.01
* 0.01–0.05
. 0.05–0.1
blank >0.1

Table 3. Parameter estimates and statistics for the catch model

Variable	Estimate	SE	z-value	*p*-value[a]	
(Intercept)	-4.3632	1.4610	-2.9860	0.0029	**
Ocean (Atlantic)	1.0613	0.5380	1.9730	0.0489	*
Ocean (Indian)	3.6139	0.7884	4.5840	0.0000	***
Depth (deep)	-3.4407	0.5581	-6.1650	0.0000	***
Depth (regular)	0.0145	0.2088	0.0690	0.9447	
Quarter II	-0.8328	0.2166	-3.8450	0.0001	***
Quarter III	-0.9085	0.1897	-4.7900	0.0000	***
Quarter IV	-0.7091	0.2555	-2.7750	0.0057	**
Exploitation years	0.0927	0.0329	2.8180	0.0050	**
Target species (MIX)[b]	-17.1967	3222.2634	-0.0050	0.9957	
Target species (SHK)[b]	-1.8695	2.9695	-0.6300	0.5292	
Target species (SWO)[b]	-0.5753	0.6871	-0.8370	0.4028	
Target species (YFT)[b]	-1.4033	0.4688	-2.9940	0.0029	**
Water depth 1	-4.4369	0.5914	-7.5020	0.0000	***
Water depth 3	-0.3809	0.3865	-0.9860	0.3247	
Water depth 4	0.2127	0.3296	0.6450	0.5190	

[a] Significance codes are defined in the footnote to Table 2
[b] Target species codes are defined in the footnote to Table 1b

Table 4. Sex ratios and statistics for crocodile shark

Dataset name	Male (no.)	Female (no.)	Ratio (%)	Chi-square statistic	*p*-value[a]	
JP Pacific yellowfin	18	3	86	9.333	0.002	**
US Pacific tuna	162	40	80	72.480	0.000	***
AU Indian swordfish	57	42	58	1.980	0.159	
SPC Pacific bigeye	69	71	49	0.007	0.933	
JP Indian yellowfin	74	78	49	0.059	0.808	
US Pacific swordfish	10	15	40	0.640	0.424	
US Atlantic swordfish	34	70	33	11.779	0.001	***
JP Southern bluefin	2	15	12	8.471	0.004	**
All data combined	426	334	56	13.950	0.000	***

[a] Significance codes are defined in the footnote to Table 2

Figure captions

Figure 1. External characteristics of the crocodile shark *Pseudocarcharias kamoharai*. A. Individual caught in the equatorial Indian Ocean in 1984 (Romanov, Zamorov, 1994). B. Pacific fixed individual from Hawaii (Randall, 1997). FAO line-drawing (Compagno, 1984).

Figure 2. Species commonly confused with crocodile shark (*P. kamoharai*). A, B. *Odontaspis noronhai*, (photo source: A. FishBase, www.fishbase.org submitted by NMFS/PIRO Observer Programs http://ias.pifsc.noaa.gov/lds/lods.html ; B. Anon., 1999), C. Squalidae species (at the photo *Scymnodon obscurus* source FishBase photo by Cambraia Duarte, Pedro Miguel Niny).

Figure 3. Global distribution of crocodile shark (P. kamoharai) as shown at Compagno, 1984.

Figure 4. Distribution records of the crocodile shark *P. kamoharai* in the Indian Ocean during SIOTLLRP, 1961-1989.

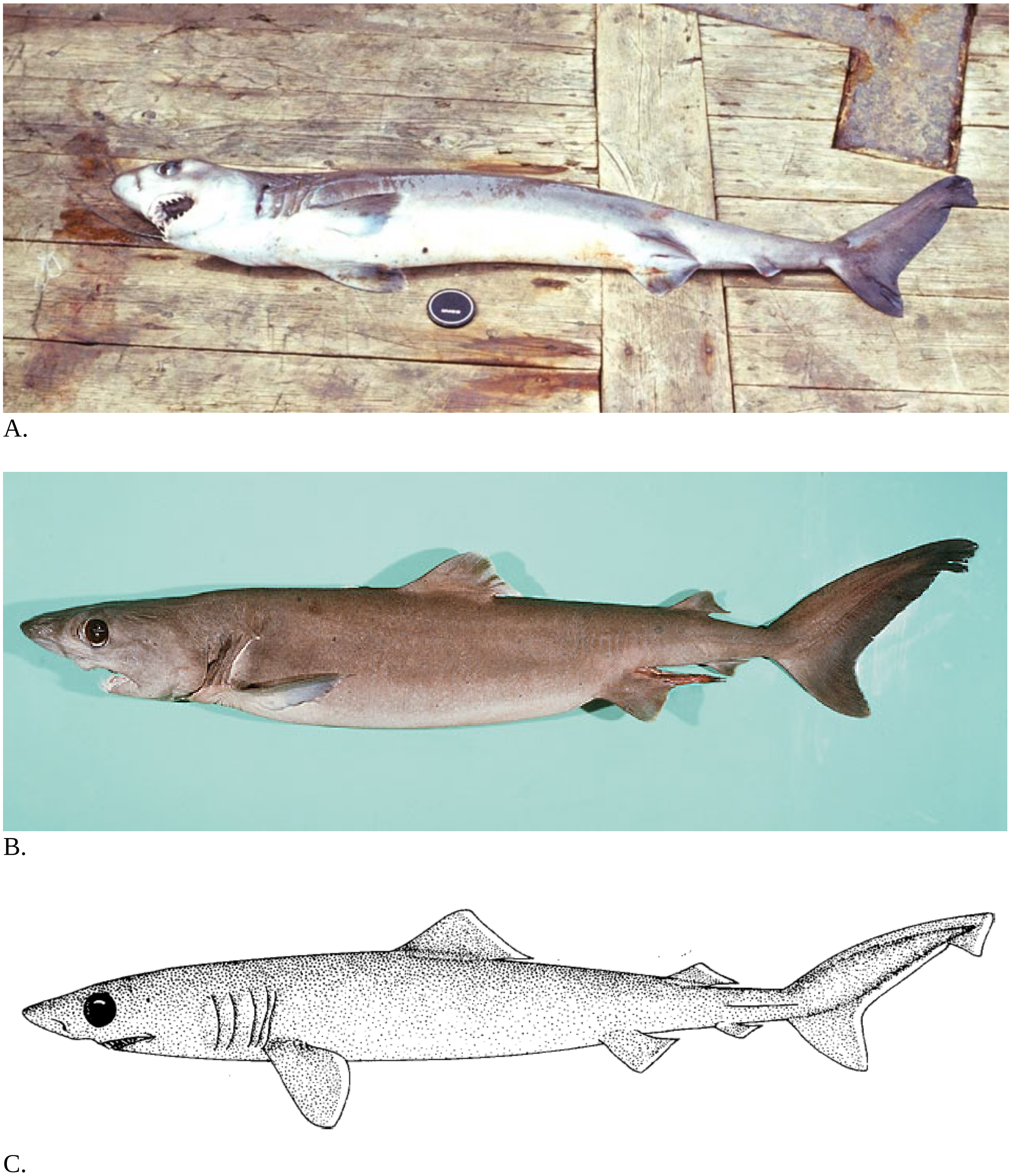
Figure 5. Distribution and relative abundance of the crocodile sharks in the Western Australia pelagic longline fisheries (early 2000s) (pictures extracted from Ward, Curran, 2004) and during Spanish experimental fishing program in the southwestern Indian Ocean in 2004-2005 (picture and data from Ariz et al, 2006). A. Spanish experimental program. B. Western Australian fisheries).

Figure 6. Global distribution of catch records of crocodile shark.

Figure 7. Length frequency histograms of crocodile shark from nine fisheries. Dark shading indicates females, light shading indicates males, and clear histograms indicate crocodile shark that were not sexed.

Figure 8. Histograms of variables modeled to explain longline catches of crocodile shark. Target species codes are defined in the footnote to the Table 1b.

Figure 9. Effect of explanatory variables on catch rates of crocodile shark. The predictions are derived from the encounter and catch models combined for a longline operation where each variable is the mean or mode of the entire dataset. For “years of longlining”, the thick line connects mean predictions for each year. For other variables, the circle indicates mean predictions.



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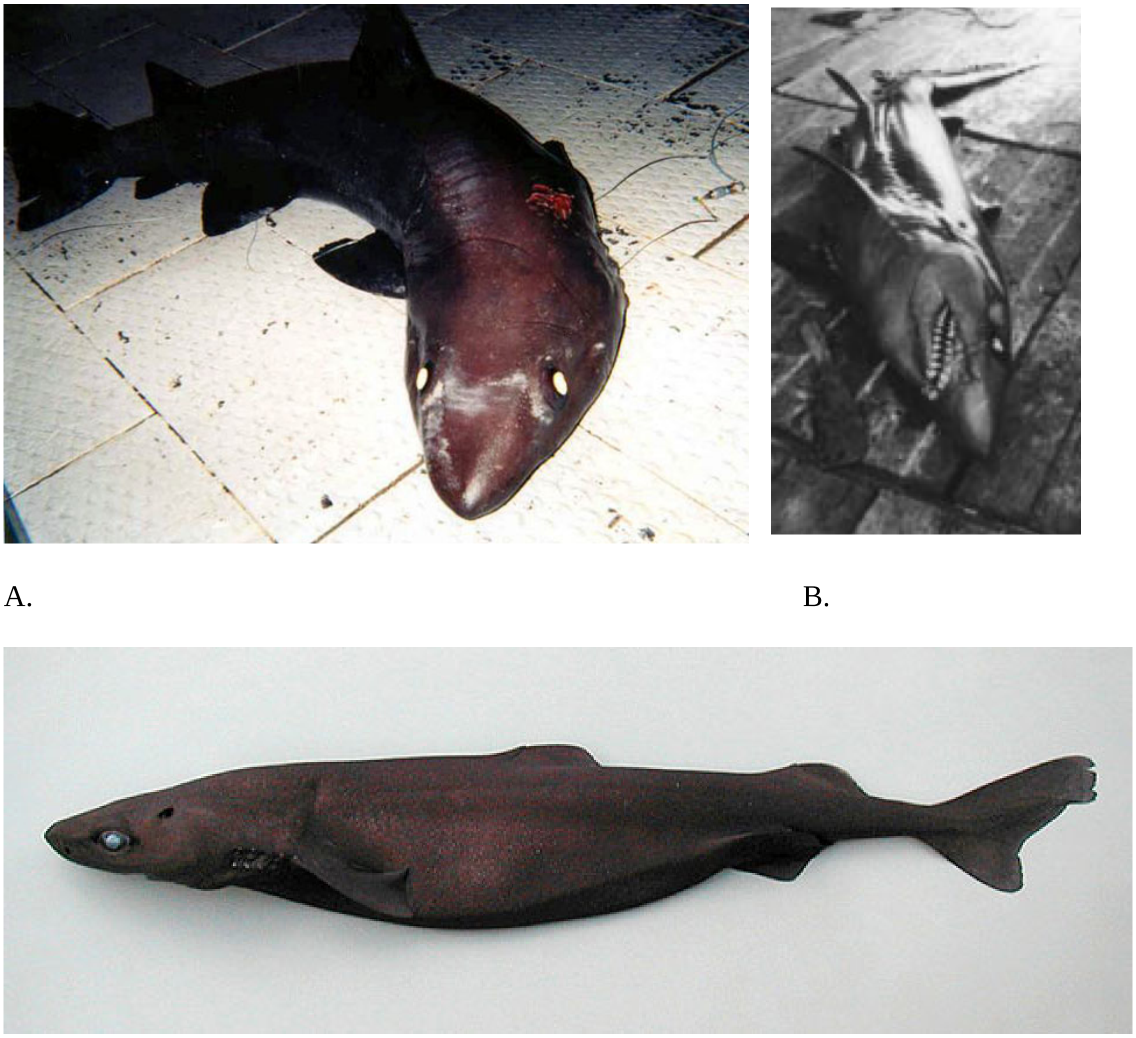

A. B.

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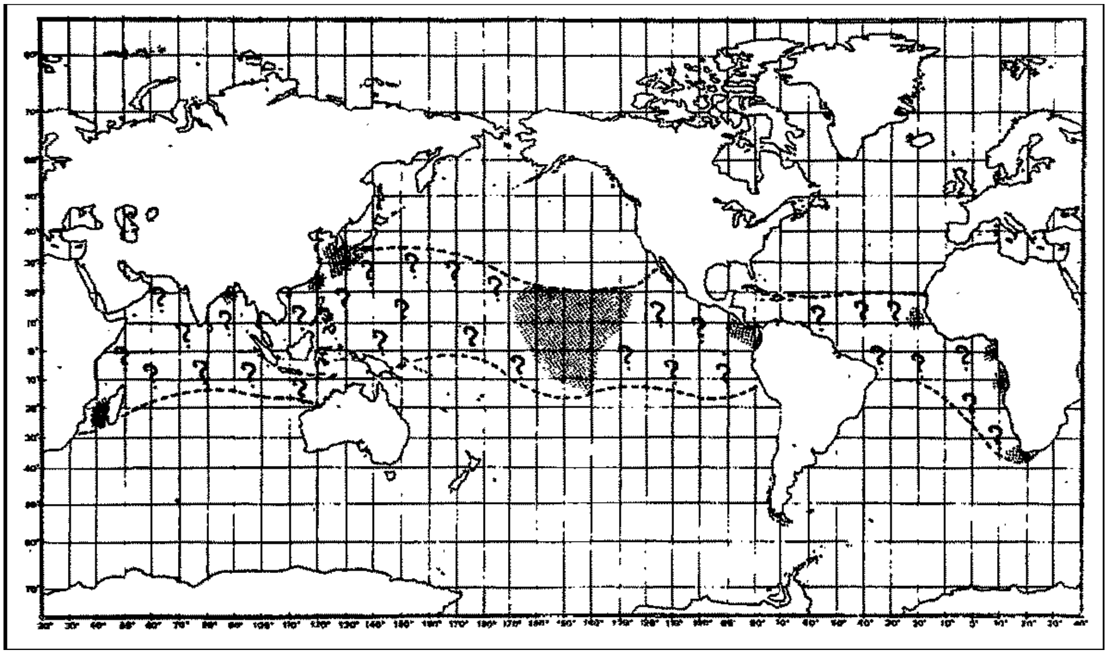

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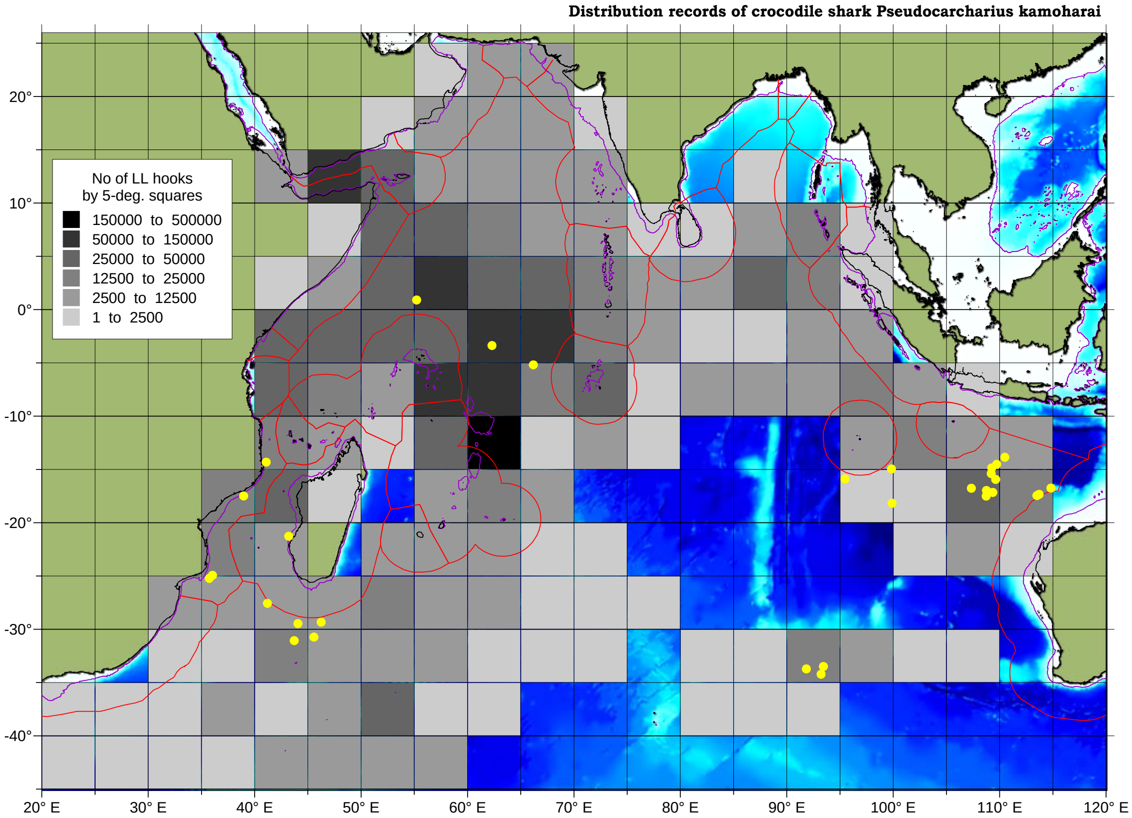
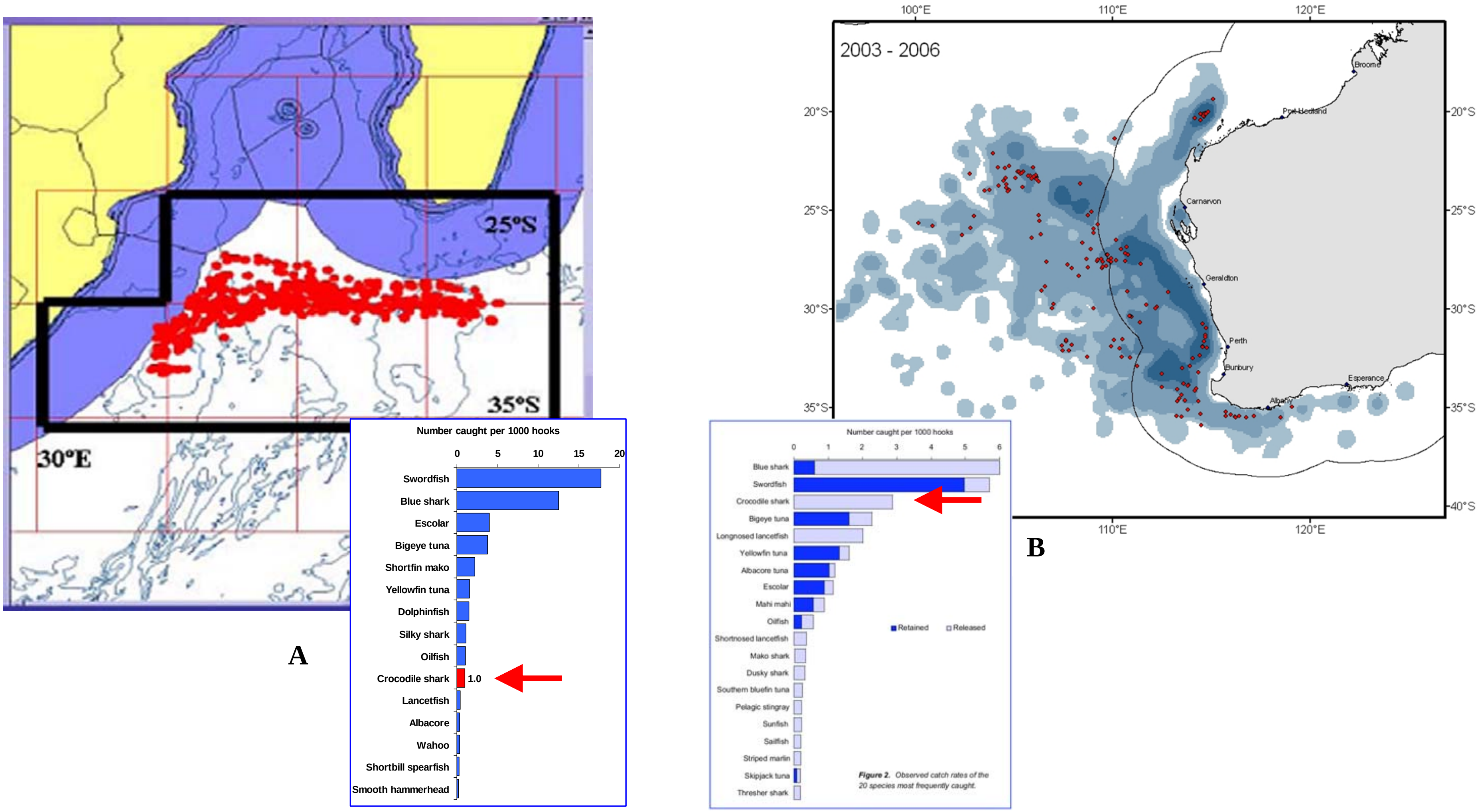


Fig. 4. Distribution records of the crocodile shark *P. kamoharai* in the Indian Ocean during SIOTLLRP, 1961-1989.



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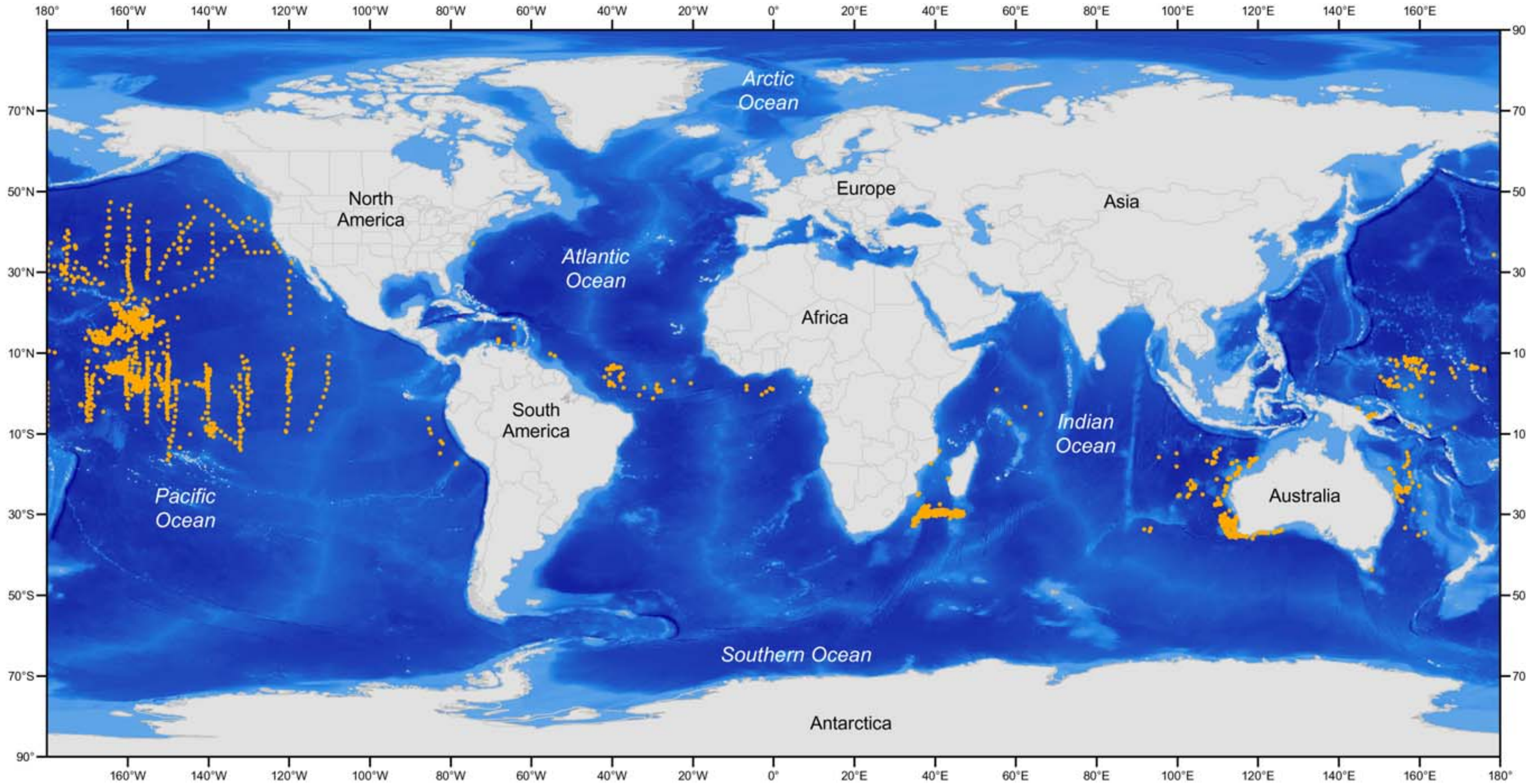

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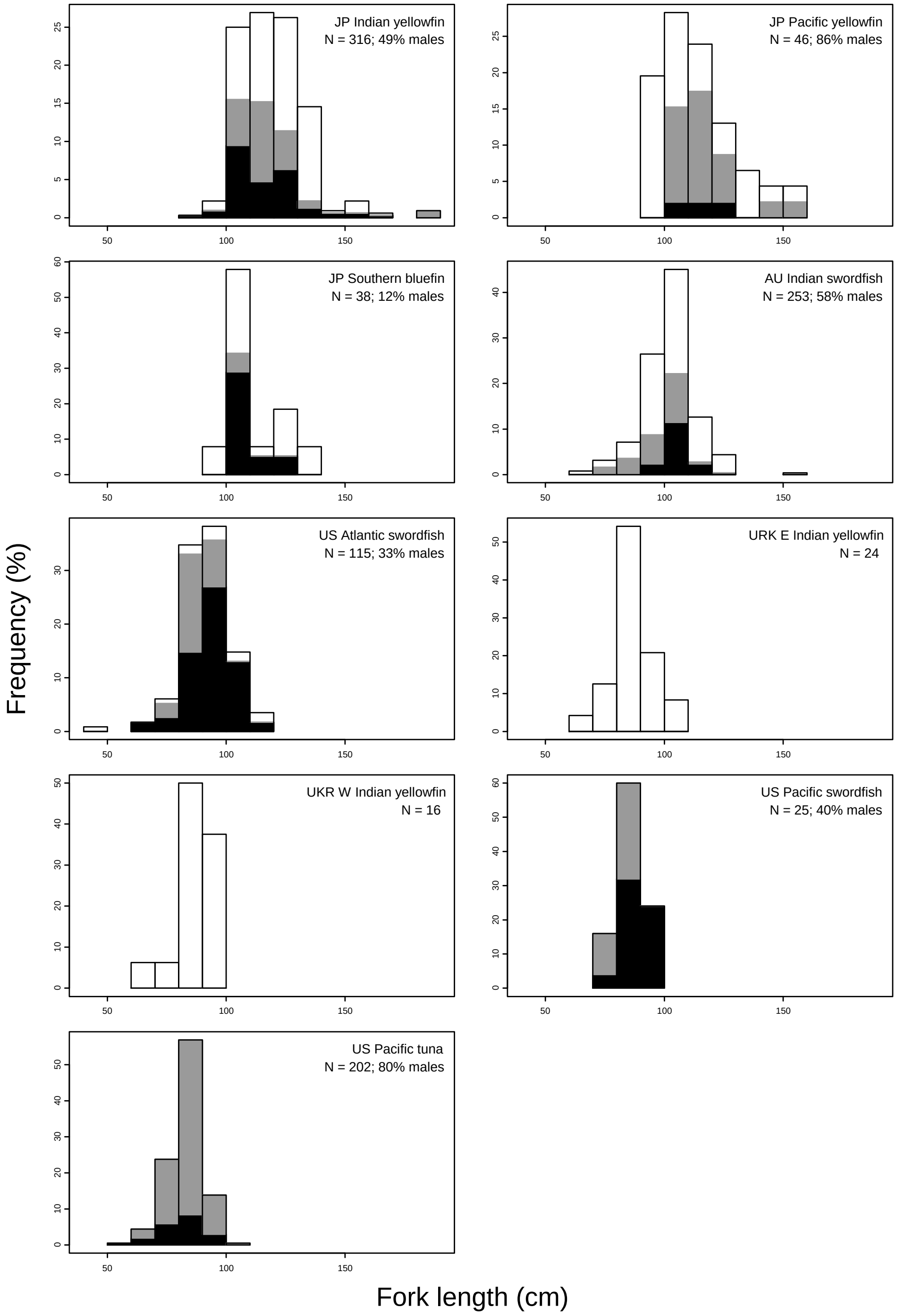

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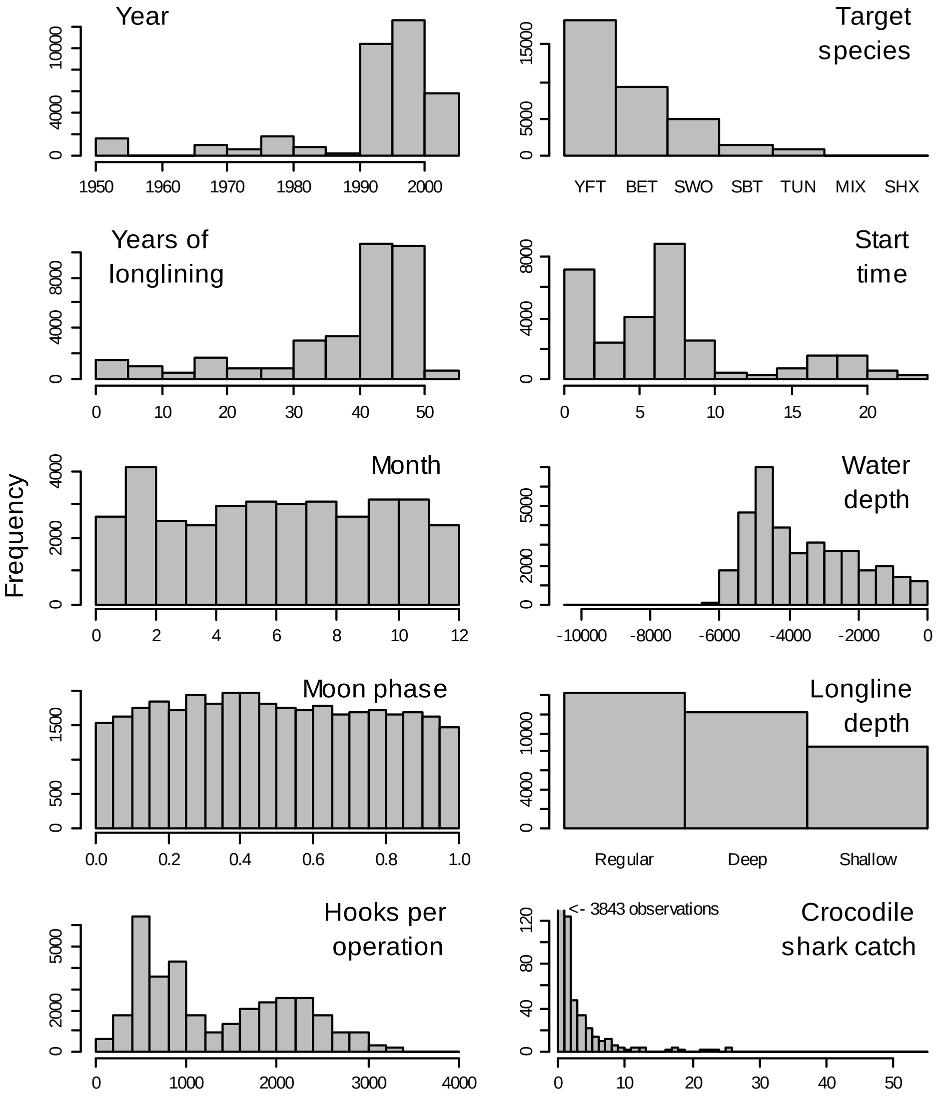

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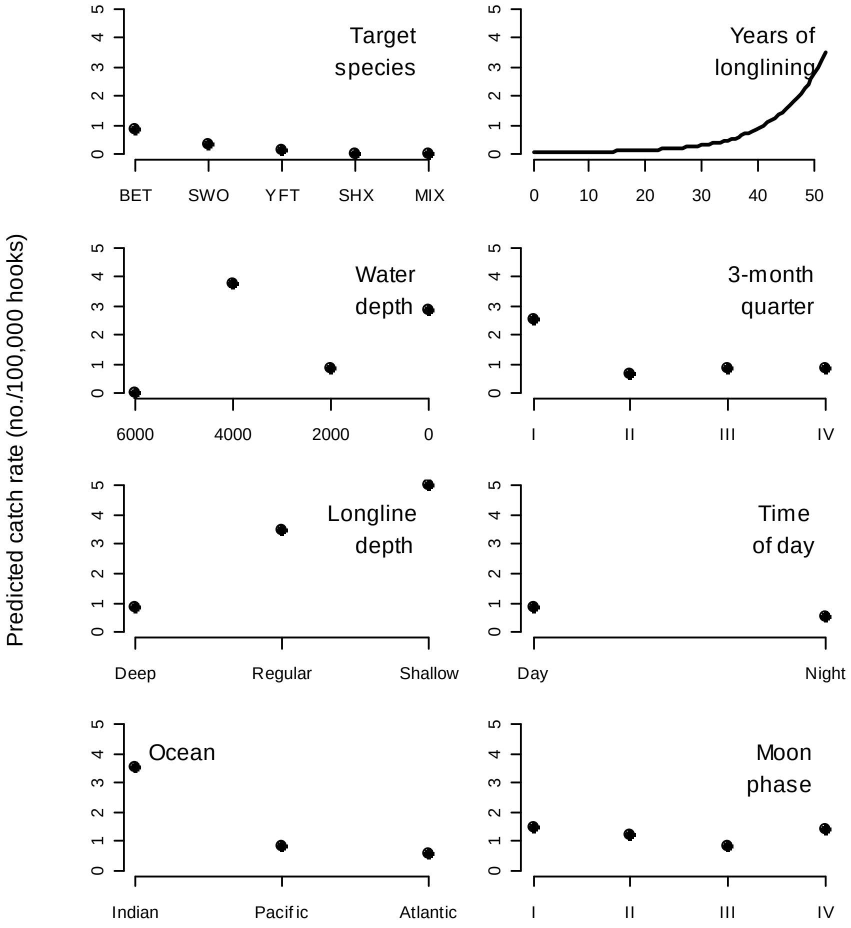

Figure 9. Effect of explanatory variables on catch rates of crocodile shark. The predictions are derived from the encounter and catch models combined for a longline operation where each variable is the mean or mode of the entire dataset. For “years of longlining”, the thick line connects mean predictions for each year. For other variables, the circle indicates mean predictions.