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Fishery-dependent biological observations of the crocodile shark, *Pseudocarcharias kamoharai*, from the southeast coast of India

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ABSTRACT. The crocodile shark, *Pseudocarcharias kamoharai*, is widely distributed in tropical and subtropical oceans but remains poorly documented in the northern Indian Ocean. We report fishery-dependent biological observations from 46 specimens landed as retained bycatch at Kakinada and Chennai, India, between March 2023 and February 2025. Total length ranged from 73.2 to 102.0 cm and total weight from 1,280 to 5,260 g. The overall length-weight relationship (LWR) was $TW = 0.001045 \cdot TL^{3.280}$ ($R^2 = 0.774$). Two-tailed t-tests indicated isometric growth ($b = 3$) for combined samples, males ($b = 2.685$), and females ($b = 3.511$). Maturity transition bounds were established at 82.0-82.5 cm TL for males and 83.0-84.0 cm TL for females. One pregnant female measuring 97.2 cm total length and weighing 4,220 g carried four advanced embryos (32.7-35.5 cm TL). Stomach observations were available for 25 specimens, of which seven contained identifiable food remains, including squid, shrimp and pufferfish. These observations expand the biological dataset available for *P. kamoharai* in the Bay of Bengal and support continued monitoring of fishery interactions, retention and discard mortality in the region.

Key words: Pelagic longline, bycatch, maturity, reproductive biology, length-weight relationship.

Observaciones biológicas del tiburón cocodrilo *Pseudocarcharias kamoharai*, relacionadas a la pesca, en la costa sureste de la India



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RESUMEN. El tiburón cocodrilo, *Pseudocarcharias kamoharai*, está ampliamente distribuido en océanos tropicales y subtropicales, pero aún está poco documentado en el norte del Océano Índico. Presentamos observaciones biológicas dependientes de la pesca de 46 especímenes desembarcados como captura incidental retenida en Kakinada y Chennai, India, entre marzo de 2023 y febrero de 2025. La talla total osciló entre 73,2 y 102,0 cm y el peso total entre 1.280 y 5.260 g. La relación talla-peso (LWR) general fue $TW = 0,001045 \cdot TL^{3,280}$ ($R^2 = 0,774$). Las pruebas t de dos colas indicaron crecimiento isométrico ($b = 3$) para muestras combinadas, machos ($b = 2,685$) y hembras ($b = 3,511$). Se establecieron límites de transición a la madurez en 82,0-82,5 cm TL para los machos y 83,0-84,0 cm TL para las hembras. Una hembra preñada, con una talla total de 97,2 cm y un peso de 4.220 g, portaba cuatro embriones avanzados (32,7-35,5 cm TL). Se obtuvieron observaciones estomacales de 25 especímenes, de los cuales siete contenían restos de alimento identificables, incluyendo calamares, camarones y peces globo. Estas observaciones amplían el conjunto de datos biológicos disponibles para *P. kamoharai* en la Bahía de Bengala y respaldan el monitoreo continuo de las interacciones con la pesca, la retención y la mortalidad por descarte en la región.

Palabras clave: Palangre pelágico, captura incidental, madurez, biología reproductiva, relación talla-peso.

The monotypic family Pseudocarchariidae (order Lamniformes) comprises a single species, the crocodile shark *Pseudocarcharias kamoharai* (Matsubara, 1936), distributed throughout tropical and subtropical waters globally (Compagno 2001; Wu et al. 2020). This epipelagic and mesopelagic shark is characterized by its distinctively large eyes, a pointed snout, long gill slits, and rows of slender, sharp teeth. Its diet consists primarily of small pelagic fishes (e.g. Myctophidae, Gonostomatidae), benthic crustaceans, shrimps, squids and mesopelagic cephalopods (Compagno 2001; Calle-Morán et al. 2022). Bathymetrically, this species spans from the surface down to depths exceeding 600 m, exhibiting a distinct diel vertical migration pattern characterized by nocturnal foraging in shallower epipelagic zones (Walker and Gason 2007; Ebert et al. 2013). Despite its circumtropical distribution, the species is frequently taken as bycatch in commercial pelagic longline fisheries targeting swordfish and tuna but are usually discarded (Silambarasan et al. 2023; John et al. 2025), and their catch data are often under-reported or omitted from logbook records (Kyne et al. 2019).

Within the Indian EEZ, confirmed records remain fragmented but geographically widespread across both coastlines. The species was documented along the Chennai coast (Kizhakudan et al. 2013), followed by occurrences along the southwestern coast in the Arabian Sea (Akhilesh et al. 2013), the deep waters of the Andaman Sea (Pradeep et al. 2017), the Gulf of Mannar (Kannan et al. 2019), off Visakhapatnam, Andhra Pradesh (Silambarasan et al. 2023), and Cochin (John et al. 2025). While recent studies (e.g. John et al. 2025) have documented initial occurrence, biological parameters from the northern Indian Ocean remain limited. This study provides baseline biological information on *P. kamoharai* along the southeast coast of India, including length-weight dynamics, empirical maturity bounds, uterine fecundity and stomach contents. Because sampling relied on fishery-dependent, opportunistically retained specimens rather than a probability sample, results are

interpreted as characteristics of the sampled landings rather than population-level estimates.

A total of 46 specimens of *P. kamoharai* were collected opportunistically between March 2023 and February 2025 from retained commercial bycatch landed at two major fishing harbours on India's east coast: Kumbhabhishekam (Kakinada, Andhra Pradesh; n = 40) and Kasimedu (Chennai, Tamil Nadu; n = 6) (Table 1; Figure 1). Specimens landed at Kakinada originated from pelagic longline and deep-water drift gillnet operations conducted approximately 100 km offshore at depths of 300-400 m. Targeted species in these fisheries included pelagic teleosts such as *Thunnus* spp. and *Xiphias gladius*, using pelagic longlines (equipped with circle hooks baited with teleosts or squids) and drift gillnets with stretched mesh sizes of 140-180 mm. Precise geographic capture locations could not be determined due to the fishery-dependent nature of the sampling. Although non-targeted and historically discarded, retained individuals are sold locally for low-cost human consumption, fishmeal production, or liver oil extraction. Species identification followed Compagno et al. (2005). Total length (TL, cm), total weight (TW, g), and sex were recorded at landing sites. Laboratory dissections were performed on a subset (n = 25) to assess reproductive organs and stomach contents. LWR parameters were estimated by ordinary least-squares linear regression of natural log-transformed data (ln, base e):

$$\ln(TW) = \ln(a) + b \ln(TL)$$

Isometric growth ($H_0: b = 3$) was tested using two-tailed Student's t-test: $t = (b - 3)/SE_b$. An ANCOVA incorporating $\ln(TL)$, sex, and their interaction evaluated slope parallelism between sexes. Sex differences in TL were assessed with the Mann-Whitney U-test and sex ratio was tested against an expected 1:1 ratio using a chi-square goodness-of-fit test, acknowledging possible selective-retention bias at the sample level. Significance was set at $\alpha = 0.05$, with emphasis on effect sizes

Table 1. Summary of biological measurements for *Pseudocarcharias kamoharai* sampled from bycatch landings along the south-east coast of India.

Parameter	Combined (n = 46)	Males (n = 27)	Females (n = 19)
Total length range (cm)	73.2-102.0	75.3-102.0	73.2-102.0
Mean length $\pm$ SD (cm)	89.4 $\pm$ 7.2	89.1 $\pm$ 6.8	89.8 $\pm$ 7.9
Total weight range (g)	1,280-5,260	1,556-3,342	1,280-5,260
Mean weight $\pm$ SD (g)	2,784 $\pm$ 812	2,542 $\pm$ 465	3,128 $\pm$ 1,075
Clasper length range (cm)	-	5.6-7.6	-
Smallest observed mature (cm TL)	-	82.5	84.0
Largest observed immature (cm TL)	-	82.0	83.0

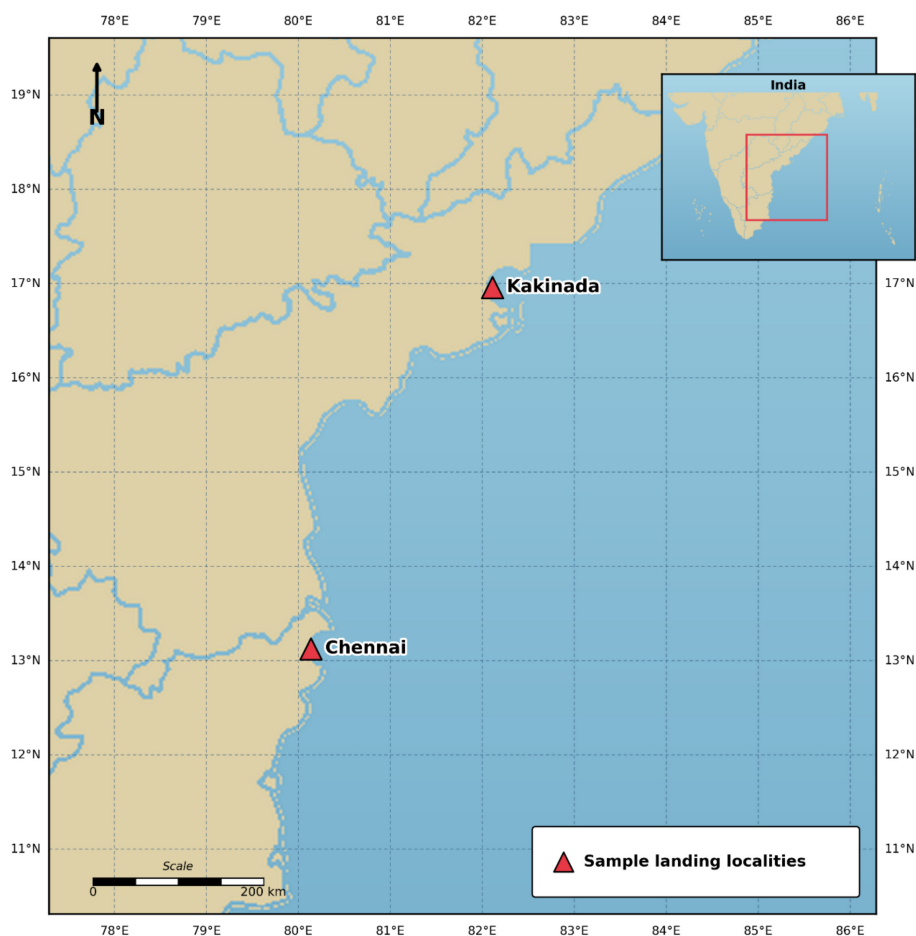


Figure 1. Landing localities for *Pseudocarcharias kamoharai* along the southeast coast of India: Kakinada, Andhra Pradesh, and Chennai, Tamil Nadu. Markers indicate fish-landing centres where specimens were retained, not the capture locations. Inset: location of the study area within India.

and 95% confidence intervals. All analyses were performed in Python 3.12.3 using NumPy 2.4.4, pandas 3.0.2, SciPy 1.17.1, and Matplotlib 3.10.8. Male maturity was assessed macroscopically for all specimens using external clasper length and calcification/rigidity. Testis development was additionally examined in the dissected subset ($n = 6$). Female maturity was assessed in dissected specimens ($n = 19$) based on ovarian follicle diameter and uterine condition. Maturity status was recorded as a binary classification (immature/mature) and plotted against TL separately by sex. Because immature and mature length distributions were completely separated, logistic maximum-likelihood estimation of L_{50} was not feasible, so empirical transition bounds (largest immature to smallest, mature individual) and their midpoints were reported instead. Stomach contents were examined visually. The high prevalence of empty stomachs and heavily digested prey precluded genus- or species-level dietary identification, so prey items were grouped into broad taxonomic categories.

The combined sample comprised 46 crocodile

sharks ranging from 73.2 to 102.0 cm TL and 1,280 to 5,260 g. The sample included 27 males and 19 females (M:F = 1.42:1); males ranged from 75.3 to 102.0 cm TL, and females from 73.2 to 102.0 cm TL. Individuals measuring 82–96 cm represented 76.1% (35/46) of the sample (length-frequency counts by 5 cm class, 73.2–77.9 cm: $n = 2$; 78.0–82.9 cm: $n = 7$; 83.0–87.9 cm: $n = 14$; 88.0–92.9 cm: $n = 10$; 93.0–97.9 cm: $n = 9$; 98.0–102.0 cm: $n = 4$). A *Chi*-square test against an expected 1:1 ratio was not significant ($\chi^2 = 1.39$, $df = 1$, $p = 0.238$) and the Mann-Whitney test detected no evidence of a difference in TL distributions between sexes ($U = 181.0$, $p = 0.094$).

Observed ranges overlapped substantially, and both sexes reached 102.0 cm TL; the greater body mass of one 102.0-cm female (5,260 g) than one 102.0-cm male (3,342 g) is an individual observation, not evidence of sex-specific growth, and applies only to this retained sample. The combined length-weight regression equation was $TW = 0.001045 \cdot TL^{3.280}$ ($R^2 = 0.774$, $SE_b = 0.258$, 95% CI: [2.76, 3.80]) (Figure 2). Sex-specific regressions

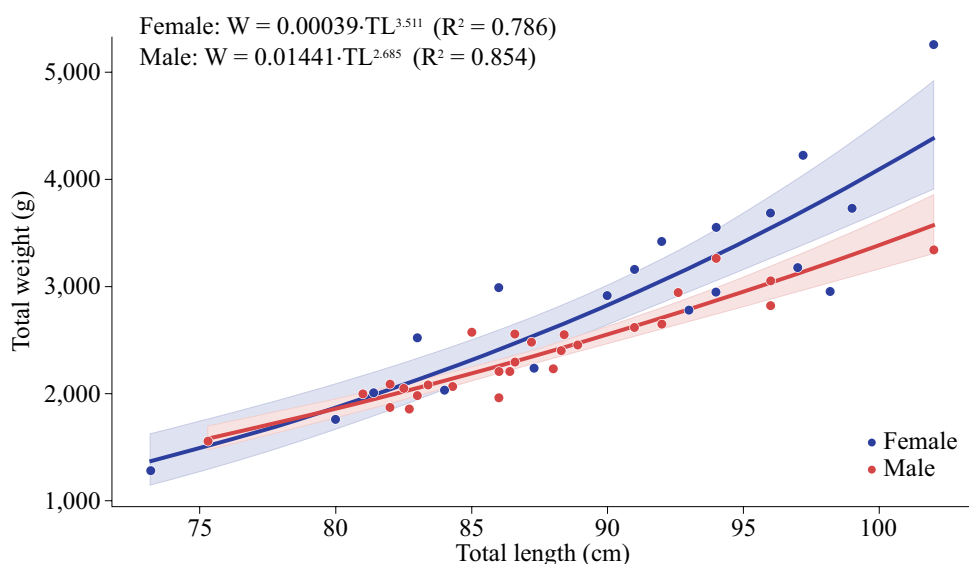


Figure 2. Length-weight relationships for *Pseudocarcharias kamoharai* specimens landed at Kakinada and Chennai, India, between March 2023 and February 2025. Body mass is expressed in grams and total length in centimetres. Individual observations are shown for males ($n = 27$) and females ($n = 19$). Fitted power curves ($W = aTL^b$) are shown separately for males and females; shaded bands represent the 95% confidence interval of each regression.

yielded $b = 2.685$ ($R^2 = 0.854$, $SE_b = 0.231$) for males and $b = 3.511$ ($R^2 = 0.786$, $SE_b = 0.327$) for females (Table 2). Two-tailed t-tests confirmed isometric growth ($b = 3$) for combined ($t = 1.085$, $p = 0.284$), male ($t = -1.364$, $p = 0.185$), and female ($t = 1.563$, $p = 0.136$) cohorts. ANCOVA revealed no significant difference between male and female slopes ($F(1,42) = 3.95$, $p = 0.053$).

Mature individuals comprised 82.6% ($n = 38$) of the total sample. Clasper lengths ranged from 5.6 to 7.6 cm; testis lengths varied from 5.1 to 9.1 cm. Four males were immature and 23 mature, whereas

four females were immature and 15 mature (85.2% and 78.9% mature, respectively). Male maturity transition occurred between 82.0 cm (largest immature) and 82.5 cm TL (smallest mature), with an empirical midpoint of 82.25 cm TL. Female transition occurred between 83.0 cm and 84.0 cm (midpoint: 83.50 cm TL) (Figure 3). These midpoints are descriptive summaries only, not estimates of population L_{50} , since no specimens fell within the transition gaps and sampling was opportunistic and non-probabilistic (Figure 3). One female measuring 97.2 cm TL (4,220 g) carried four advanced

Table 2. Estimated length-weight relationship (LWR) parameters for males, females, and the combined samples of *Pseudocarcharias kamoharai* from the Bay of Bengal. Sample sizes (n), regression coefficients (Intercept a and Slope b), 95% CI of b , standard error (SE_b), and coefficients of determination (R^2) are provided for each cohort.

Group	n	a	b	CI	SE_b	R^2
Combined	46	0.001045	3.28	[2.76, 3.80]	0.258	0.774
Males	27	0.014408	2.685	[2.21, 3.16]	0.231	0.854
Females	19	0.000389	3.511	[2.82, 4.20]	0.327	0.786

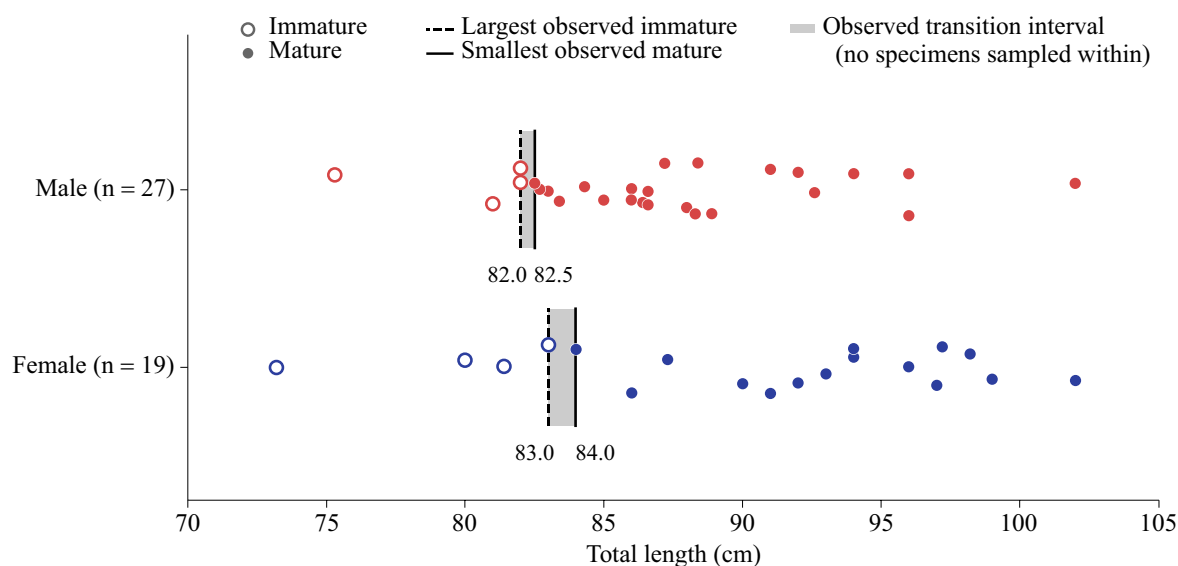


Figure 3. Observed maturity status in relation to total length for male and female *Pseudocarcharias kamoharai*. The shaded region indicates the interval between the largest observed immature and smallest observed mature individual for each sex. The observed male transition interval was 82.0-82.5 cm TL, and the female transition interval was 83.0-84.0 cm TL. No logistic maturity curve or population L_{50} estimate is shown because maturity status was completely separated by length.

embryos (two per uterus) (Figure 4 D). The right uterus contained two male embryos (34.6 cm TL; 194 g and 35.5 cm TL; 208 g), and the left uterus contained two female embryos (32.7 cm TL; 189 g and 34.1 cm TL; 227 g). Embryos had fully developed fins, large eyes, and internal yolk remnants (Figure 4 E). The litter size of four and the embryonic metrics are consistent with the oophagous

reproductive strategy described globally for this species (Oliveira et al. 2010; Dai et al. 2012).

Stomach contents were examined in 25 specimens, with 18 (72%) being empty or containing unidentifiable digestive fluid. Total stomach weights varied widely, ranging from 28 to 296 g. Only seven stomachs contained identifiable remains (Table 3). Because prey items were not quantified using



Figure 4. Reproductive images of *Pseudocarcharias kamoharai*. A) Mature male with testes (TL 86.4 cm), PK-22, Chennai, 9 March 2024. B and C) Mature females carrying eggs, PK-11, PK-18, Kakinada, February 2025. D) Mature female (TL-97.2 cm) with embryos ($n = 4$) inside the uterus, Chennai, PK-23, 9 March 2024. E) Fully developed embryo (female, 34.1 cm TL) with yolk sac remnants. Scale bar = 5 cm. All images © Sweta Beura.

Table 3. Per-specimen stomach content records for *P. kamoharai* specimens with identifiable prey remains. Total length (TL, cm) and weights (g) are given per individual prey item. M: male. F: female.

Stomach no.	Specimen ID	TL	Sex	Landing site	Fullness	Identifiable contents	Weight
1	PK-21	88.3	M	Kakinada	1/4	1 Squid beak	0.94
2	PK-18	73.2	F	Kakinada	1/3	Squid tissue remains	0.33
3	PK-17	87.3	F	Kakinada	Trace	1 Squid beak	0.23
4	PK-14	96.0	F	Chennai	Full	2 Squid mantle	42, 29
						2 Semi-digested shrimp	33, 22
						2 shrimp heads	9, 11
5	PK-19	98.2	F	Kakinada	3/4	1 semi-digested pufferfish	25
6	PK-22	86.6	M	Kakinada	Trace	Squid head	0.10
7	PK-20	82.7	M	Kakinada	Trace	Digested shrimp remains	0.19

standardized frequency, occurrence or mass methods, these observations are presented descriptively and do not support conclusions about diet dominance or specialization.

The crocodile shark is a secondary bycatch species in pelagic longline fisheries targeting swordfish and tunas across the world's oceans (Romanov et al. 2008). It has low biological productivity that may increase susceptibility to gear interactions; however, this study does not assign a vulnerability rank or demonstrate that this species is the most vulnerable pelagic shark. It commands low commercial value; landed specimens are frequently retained to utilize their fins, meat, and squalene-rich liver oil.

Previous Indian studies document *P. kamoharai* from several coastal regions, and John et al. (2025) reported nine specimens from India (collected at Kochi but captured from Maldives waters), including a gravid female (102 cm TL) with four embryos. The present study adds observations from retained specimens and provides additional information on length, mass, sex, maturity and stomach contents. The pregnant female (97.2 cm TL) provides an additional Indian observation consistent with the reproductive pattern previously reported for this species. The size frequency and field observations indicated that landings consisted mainly of mature

individuals of both sexes, representing a major proportion of the retained sample. The male-biased composition observed cannot be used to infer population-level sex dominance or spatial or sexual segregation because sampling was opportunistic and lacked standardized effort, gear-specific sampling and trip-level independence. Despite our relatively modest sample size, these data strongly agree with established global life-history assessments. Continued monitoring should record gear type, fishing effort, depth, location, number captured, condition at capture, retention and discard outcome. These data are needed to evaluate fishery interactions and support regional conservation planning.

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Conflict of interest

The authors declare no conflict of interest.

Author contributions

Sweta Beura performed writing-original draft and conceptualization; data curation; formal analysis; methodology; resources. K. K. Bineesh performed supervision; validation; writing-review and editing; conceptualization.

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