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Insights in to reproductive dynamics and feeding biology of *Sphyraena putnamae* Jordan and Seale, 1905 exploited in the Indian EEZ

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Abstract

The sawtooth barracuda *Sphyraena putnamae*, widely distributed in the Indo-Pacific region, is one of the commercially important barracuda species exploited by trawls in the Indian EEZ. The present study examined 2,135 *S. putnamae* collected during 2014-2020 from different fish landing centres along the Indian coast, to elucidate their reproductive and feeding behaviour. The fork length of sampled females and males varied from 12.5 to 130.9 cm and 16.5 to 90.0 cm respectively. Negative allometric growth was observed with a significant difference (p<0.05) between the sexes. The observed sex ratio (Female:Male) was 1.23:1, indicating the dominance of females. Size at sexual maturity for females and males were estimated at 55.3 and 45.4 cm fork length respectively. The higher proportion of spawning capable individuals and higher gonadosomatic index (GSI) values in females observed during March to May and November-December revealed the bimodal and protracted spawning nature of this species. Absolute fecundity increased with fork length and weight and varied from 70,080 to 10,18,068 oocytes with an average of 3,16,568 oocytes. The stomach vacuity index of females and males was 49.09 and 47.92% respectively. Fifty-nine prey items were identified in the diet, with a predominance of fishes confirming *S. putnamae* has a piscivorous feeding behaviour.

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Introduction

The sawtooth barracuda *Sphyraena putnamae* Jordan and Seale, 1905 is one of the commercially important barracuda species exploited by trawls in the Indian EEZ. The barracudas, otherwise called spikes, belong to the family Sphyraenidae. They are represented by a single genus *Sphyraena* including 27 species (Nelson *et al*., 2016). Of these, eleven species exist in Indian waters, which include, *Sphyraena acutipinnis, S. barracuda, S. jello, S. putnamae, S. qenie, S. forsteri, S. obtusata, S. flavicauda, S. chrysostaenia, S. helleri* and *S. arabiansis* (Eschmeyer and Fong, 2017). Barracudas are important food as well as sport fish and are found in both tropical and subtropical regions. Many researchers have studied and reported the feeding biology of barracudas such as *S. barracuda* populating the Florida Bay (De Sylva, 1963; Hansen, 2015), East African waters (Williams, 1965), the Indian Ocean and adjacent seas (De Sylva, 1973) and the Kosi system of northern Zululand (Blaber, 1982); *S. chrysotaenia, S. flavicauda* and *S. sphyraena* from the Egyptian Mediterranean waters of Alexandria (Allam *et al*., 1999); *S. jello* from the north-west of the Persian Gulf (Hosseini *et al*., 2009) and Pakistan (Manzoor *et al*., 2019); *S. putnamae* from the Persian Gulf (Mohammadizadeh *et al*., 2010); *S. viridensis*, *S. sphyraena* and *S. chrysotaenia* from Rhodes Island (Kalogirou *et al*., 2012); *S. ensis* from the Gulf of California (Moreno-Sanchez *et al*., 2019); *S. chrysotaenia* and *S. flavicauda* from the Gulf of Suez (Osman *et al*., 2019). Along the Indian coast, most of the studies conducted were on the taxonomy of barracudas (Dutt and Rao, 1967; Jones and Kumaran, 1968; De Sylva, 1973; Rao, 1973; Kothare, 1973; Kothare and Bal, 1975; Pillai and Mahadevan, 1981; Kasim and Balasubramanian, 1990; Kasim 2000). Studies on the fishery and biology of barracudas are limited in Indian waters and include reports on *S. obtusata* from the Gulf of Mannar (Somavanshi, 1989), Tuticorin (Kasim and Balasubramanian, 1990), Kerala (Premalatha and Manojkumar, 1990; Najmudeen *et al*., 2015), Mumbai (Jaiswar *et al*., 2004), Karnataka (Rajesh *et al*., 2021a; Meshram *et al*., 2021), Pamban waters of Gulf of Mannar (Vinothkumar *et al.,* 2022a, b); *S. jello* from Kerala (Premalatha and Manojkumar, 1990) and *S. putnamae* from the Arabian Sea (Rajesh *et al*. (2020a; 2021b) and from the Bay of Bengal (Ghosh *et al*., 2021a, b).

Though the barracuda fishery in India is constituted of 11 species, only four species *viz., S. obtusata*, *S. barracuda*, *S. forsteri* and *S. jello* contributed to the commercial fisheries (Kasim, 2000). However, Froese and Pauly (2019) reported that the following five species *viz., S. jello* (Cuvier, 1829), *S. obtusata* (Cuvier, 1829), *S. barracuda* (Edwards, 1771), *S. putnamae* (Jordan and Seale, 1905) and *S. qenie* (Klunzinger, 1870) were commercially important species in the Indian fishery.

Despite its wide distribution and economic significance, only limited studies are available on *S. putnamae*, which include fishery and distribution (Randall *et al*., 1990), basic aspects of food and feeding in Iranian waters (Mohammadizadeh *et al*., 2010), and reproductive and feeding biology off Karnataka from Arabian Sea (Rajesh *et al*., 2020a; 2021b) and off Andhra Pradesh from Bay of Bengal (Ghosh *et al*., 2021a, b). A comprehensive study on the feeding and reproductive biology of this species at regional level has not been attempted so far. Hence, this study on the feeding and reproductive characteristics of *S. putnamae* on a national scale was taken up, to ascertain the ecological significance of this species in Indian waters, and to provide baseline information to frame biological reference points for sustainable exploitation of the resource.

Materials and methods

Fish sampling and laboratory handling

Samples of *S. putnamae* (n=2135) were collected every month between January 2014 to December 2020 from landing centers located in Tamil Nadu [Kasimedu Fishing Harbour (13.128°N; 80.297°E) and Pamban Therkuvadi (9.279°N; 79.205°E)]; Kerala [Vizhinjam (8.3932°N; 77.0046°E), Cochin Fisheries Harbour (10.024°N; 76.462°E), Munambam Fisheries Harbour (10.434°N; 76.238°E), Kalamukku (10.240°N; 76.390°E) and Chellanam (10.047°N; 76.419°E)]; Karnataka [Mangaluru (12.853°N; 74.833°E) and Malpe (13.347°N; 74.701°E) fishing harbours]; Maharashtra [Sassoon Dock (18.909°N; 72.826°E)] and Andhra Pradesh [Visakhapatnam (17.696°N; 83.301°E), Kakinada (16.984°N; 82.279°E), Pudimadaka (17.491°N; 83.004°E), Dummulapeta (16.958°N; 82.273°E) and Bhairavapalem (16.733°N; 82.319°E)] located along the Indian coast (Fig. 1). The collected specimens were immediately placed in insulated ice boxes and then transported to the laboratory for further analyses. Fork length (FL) was measured to the nearest millimeter (mm) and total weight (W) to 0.1 g precision. The mean FL in each month was recorded. Sex of the fish sampled was identified by visual examination of the gonads, after dissecting the fishes. Fork lengths for each sex were grouped into 5.0-cm class intervals, and mid-lengths with the three highest frequencies were identified as primary, secondary and tertiary modes. The length-weight relationship was calculated separately for males and females as $W = a(FL)^b$ (Le Cren, 1951).

Reproductive dynamics

The study on reproductive dynamics included an analysis of sex ratio, maturity stages, gonadosomatic index (GSI), fecundity and length at maturity (Lm_{50}). Total body weight (TW) and gonad weight (GW) were measured for each specimen nearest to 0.1 g using an electronic weighing balance. The sex was identified based on macroscopic examination and the maturity states were determined through microscopic observation of gonads.

The ovaries were preserved in customised Gilson's fluid (Bagenal and Braum, 1978) to estimate the fecundity. The significant difference in sex ratio of the fish was estimated using the Chi-square test (Snedecor and Cochran, 1989) with Yates's correction factor (Zar, 1996).The reproductive stages in females were determined

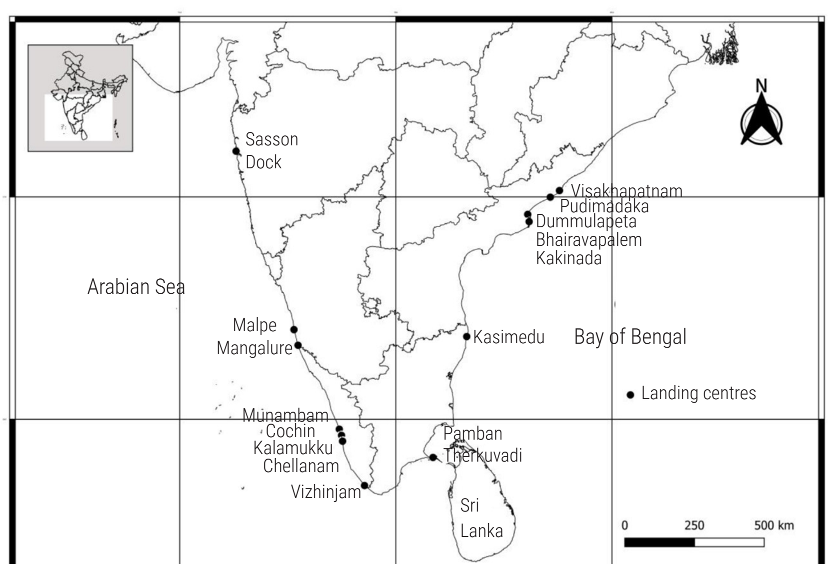

Fig. 1. Sampling locations of *S. putnamae* along Indian waters

using a five-stage maturity scale: (i) Immature, (ii) Developing, (iii) Spawning capable, (iv) Regressing and (v) Regenerating individuals as described by Brown-Peterson *et al*. (2011). The developmental phases of male and female gonads were estimated using the morphological characteristics of the ovary and testes. The spawning periodicity was assessed based on the monthly proportion (percentage) of spawning capable phases of both females and males. GSI was determined for males and females separately using the equation: GSI = (GW/SW)*100, where, GW and SW represent gonad and somatic (gutted) weights, respectively. In the annual reproductive cycle, the peak spawning season was inferred with monthly GSI values and the occurrence of various phases of gonad maturity in the reproductive cycle in different months. The proportion of mature females in the sequential length group was used for the logistic regression analysis following the model given by King (1995).

Fecundity and oocyte diameter (n=50 mature females) were estimated using the gravimetric method following the method of Murua *et al*. (2003). Subsamples (0.001 g) were taken from the anterior, middle and posterior portions of the ripe ovary and soaked in modified Gilson's solution (Simpson, 1951) for easy release of the oocytes, which were then counted. Absolute fecundity was calculated by multiplying the number of oocytes in all subsamples by the total ovary weight:

Absolute fecundity = (Weight of the ovary/Average weight of the sample)*Number of oocytes in the sample.

Relative fecundity was calculated as the number of oocytes per unit weight (g) of the fish. Using the least square method (Snedecor and Cochran, 1967), regression relation was fitted between absolute fecundity and FL and weight. For oocytes and ova diameter, a total of 300-400 oocytes were measured for their diameter from each ripe ovary using a calibrated ocular micrometer under a compound microscope.

Feeding biology

Sampled fishes were dissected and the gut was carefully removed. The degree of stomach fullness was categorised based on the distension of the stomach and the feeding intensity was classified as empty, trace, one-fourth full, half-full, three-fourth full and full (Bapat and Bal, 1958) and further classified into three different categories as: Actively feeding (three fourth full and full), Moderately feeding (half full and one-fourth full) and Low feeding (empty and trace). The fullness index (%FI) = Percentage ratio of the weight of stomach contents to the fish total body weight and the vacuity index (%V) = Percentage ratio of the empty and nearly empty stomachs to total number of stomachs analysed, were used to characterise feeding state (Chiou *et al*., 2006).

The constituents of stomach contents were analysed and ihe intact larger prey items were identified based on external morphology by using a stereomicroscope (Nikon DS-Fi2, Japan) and sorted up to their lowest possible taxonomic levels (Fischer and Whitehead, 1974; Fischer and Bianchi, 1984; Smith and Heemstra, 1986). The different prey items were observed and categorised into major taxonomic groups namely, teleosts, molluscs and crustaceans. The prey items beyond recognition due to advanced stages of digestion for which grading to taxonomic level was not possible, were classified as unidentified fish, unidentified shrimp and unidentified squids. The observed prey in each taxonomic group was counted and weighed individually to the nearest milligram using a digital electronic balance.

The index of relative importance (IRI) was estimated as per Pinkas *et al.* (1970) and the dietary coefficient (QI) following the methods of Salagado *et al*. (2004). The preferred diet of *S. putnamae* was calculated using the formula IRI = (NI+GI)×OI. The other three indices like the numerical index (NI), the occurrence index (OI) and the gravimetric index (GI) which provided the percentage of each prey item in relation to the total number, the percentage of stomachs containing a prey type in relation to the total number of stomachs with food and the percentage of each prey weight in relation to the total weight of all food content, respectively, were used for estimating the IRI and QI. For comparison, the IRI values calculated for each food item were transformed to its percentage (%IRI) values using the equation (Cortes, 1999): %IRI = 100IRI*i/n*∑*I=I* IRI*i*. Using %IRI, the prey items constituting more than 50% of the total were considered to be the preferred prey, those forming more than 25% to be the secondary prey and those constituting less than 25% to be the accessory food, as suggested by Rosecchi and Nouaze (1987). The QI of each prey item was determined using the equation: QI = NI×GI. The prey items were then classified as dominant (QI ≥ 200), secondary (QI ≥ 20 and < 200), or accidental group (QI < 20) on the basis of the calculated QI values.

Data analysis

Variation in FL distribution between females and males was evaluated using Kolmogorov-Smirnov test. Differences in the slopes of the length-weight regression for males and females were ascertained by ANCOVA, and the student's t-test was performed to observe whether the exponent (b) differed from the isometric value of 3. Month-wise homogeneity of sex ratio (1:1) was tested using Chi-square ($\chi 2$). Statistical analysis was performed using Microsoft Excel version 10.0. Differences were considered significant at an alpha level of 0.05.

Results and discussion

Fork length (FL) for females and males varied from 12.5 to 130.9 cm (mean±SE = 46.45±0.11 cm) and 16.5 to 90.0 cm (mean±SE = 40.60±0.11 cm) respectively. The weight ranged from 24.3 to 6,104 g in females and 24.3 to 3,000 g in males. A primary mode in FL composition for females and males was at 50.0 and 45.0 cm. The secondary and tertiary modes in females were at 45.0 and 40.0 cm and in males at 45.0 and 35.0 cm (Fig. 2). There was a significant difference (Z=10.6, $p<0.05$) in FL distribution between sexes. The mean FL was higher during April, December and January and lower in August, October and November (Table 1). The recorded size ranges of *S. putnamae* from the commercial landings in Indian waters were higher than that reported earlier. Letourneur *et al*. (1998) reported that the FL of *S. putnamae* ranged from 19.5 to 104.0 cm and the same length range was also reported in the New Caledonia waters by Kulbicki *et al*. (2005). Randall *et al*. (1990) reported the maximum FL for *S. putnamae* to be 90 cm TL and Mohammadizadeh *et al*. (2010) reported 93.0 cm FL both from the Great Barrier Reef and the Persian Gulf waters. Rajesh *et al*. (2020a) reported that the FL of sawtooth barracuda ranged from 18.5 to 100 cm off Karnataka coast.

Table 1. Seasonal dynamics of reproduction in *S. putnamae*

Months	Fork length (cm) (Mean ±SE) (n=2133)	Sex ratio				Spawning seasonality		
		Male	Female	F:M	χ^2 (p-value)	Spawning capable Female (%)	Spawning capable Male (%)	GSI (female) (Mean±SE)
Jan	47.28±1.17	49	78	0.76:1	2.64(0.105)	24.36	51.0	2.88±0.29
Feb	43.02±1.03	45	117	0.69:1	4.96(0.026)	28.21	44.4	2.23±0.16
Mar	45.04±0.90	102	80	0.93:1	0.30(0.583)	43.75	49.0	3.72±0.28
Apr	47.99±1.91	43	53	0.61:1	6.45(0.110)	47.17	58.1	4.22±0.52
May	43.79±1.17	75	65	0.86:1	1.15(0.283)	58.46	41.3	8.35±1.58
Jun	43.61±1.46	52	28	2.57:1	19.36(0.000)	35.71	51.9	3.08±0.31
Jul	44.23±2.22	8	23	3.52:1	67.40(0.000)	34.78	12.5	2.39±0.63
Aug	38.41±0.80	73	100	0.88:1	0.64(0.423)	17.00	28.8	1.91±0.22
Sep	45.06±0.95	132	146	1.14:1	1.03(0.310)	28.77	24.2	1.78±0.12
Oct	41.79±0.68	191	162	1.11:1	0.53(0.468)	30.86	27.2	5.08±0.79
Nov	41.20±0.55	153	148	0.84:1	2.15(0.143)	40.54	37.3	4.53±0.35
Dec	47.61±0.77	100	110	0.71:1	6.67(0.010)	45.45	41.0	4.00±0.25

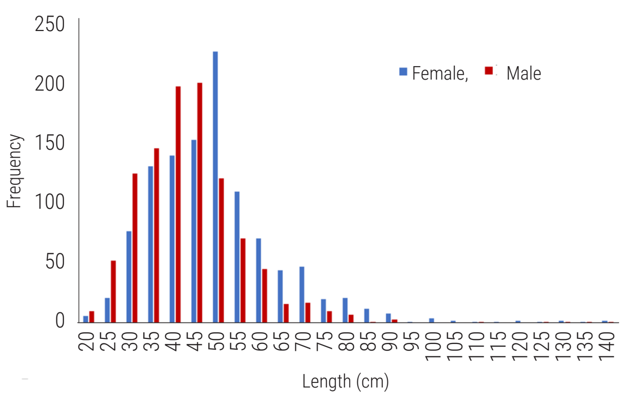

Fig. 2. Length (FL) frequencies of female and male *S. putnamae*

In Kerala waters, Roul *et al*. (2020) reported that the TL of the sawtooth barracuda ranged from 11.0 to 88.0 cm. Ghosh, *et al*. (2021a) reported that the FL of sawtooth barracuda collected from Visakhapatnam ranged from 14.7 to 123.0 cm. The variations in the size range of fishes from region to region may be attributed to the productivity of the waters and other driving factors like multi-gear and multi-species fishery, sampling localities and different fishing patterns followed in different waters (Ghosh *et al*., 2021a). Motorised crafts operating the gillnets (larger mesh size) and hook and lines (smaller hook size, No. 5-9) in Indian waters has resulted in the exploitation of larger individuals of *S. putnamae*. Higher length groups encountered in the fishery are also attributed to the differences in the fishing grounds. The smaller-sized barracudas are exploited from coastal waters and larger-sized individuals from the open waters (Whitehead *et al*., 1986).

The estimated mean FL for females and males of *S. Putnamae* in the Indian waters was higher than reported earlier especially those landed in Andhra Pradesh (Ghosh *et al*., 2021a) and Karnataka (Rajesh *et al*., 2020a). However, similar to the earlier reports from the Arabian Sea and Bay of Bengal, the mean fork length was higher in females, which implies a faster growth rate for females compared to males. In order to reproduce and develop more number of oocytes, females grow longer than males (Nikolsky, 1963).

The length-weight relationships for male, female and pooled data of *S. putnamae* are depicted in Fig. 3. The estimated coefficient "b" value based on the fork length ranged from 2.628 to 2.723, indicating a negative allometric growth of the species. There was no significant difference between the slopes (p>0.217) of males and females. This suggests that the weight for a specific FL did not vary significantly between the males and the females. (p>0.01, R^2>0.90). In general, most fishes grew more quickly in length than in weight. A similar fact was observed in *S. putnamae* and in other barracudas from different waters (Table 2). However, Kadison *et al*. (2010) reported that in barracudas, males are heavier than females and the same was observed for *S. putnamae* also. Negative allometric growth was observed in the present study, covering pan-India, with the '*b*' value of 2.666 for the pooled samples.

Females outnumbered males in all months except in June and July. Females and males constituted 51 and 49% of the total samples with an overall sex ratio (F: M) of 1.22:1 and this ratio significantly differs from the expected 1:1 ratio (chi-square df=1; p>0.01). The monthly sex ratio varied from 0.61:1 in April to 3.52:1 in July. The predominance of females in the landings was observed with sex ratios of 3.52:1 (χ^2=67.40; p>0.01), 2.57:1 (χ^2=19.36; p<0.01), 0.70:1 (χ^2=6.67; p<0.01) and 0.65:1 (χ^2=6.45; p<0.01), respectively. However, the sex ratio worked out on monthly basis revealed significant differences (Table 1).

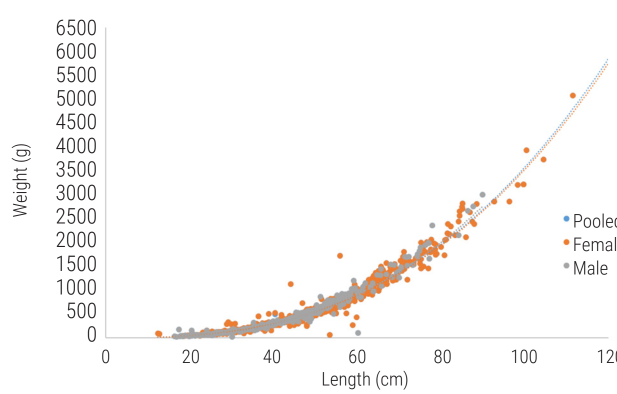

Fig. 3. Length-weight relationships inS. *Putnamae*

Table 2. Reproductive patterns in barracuda species globally (F: Female; M: Male)

Species	Slope of length-weight relation (b)	Sex ratio (F:M)	Length at sexual maturity (cm)	Spawning season	GSI (F) (max)	Absolute fecundity (Eggs) (Range)	Study area	References
Sphyraena chrysotaenia	2.8195 (F) 2.8316 (M)	1.20:1;	19.3 (F) 17.3 (M);	May-October	13.7	74,399-2,41,853	Alexandria coast, Egypt	Allam *et al*. (2004)
	-	0.84:1	19.5 (F) 19.7 (M)	August-November	-	-	Central Mediterranean	Rim *et al.* (2009)
Sphyraena flavicauda	2.730 (Unsexed)	0.54:1	28.0 (F) 25.5 (M)	May-September	7.9	84,197-2,60,549	Alexandria coast, Egypt	Allam *et al*. (2004)
Sphyraena obtusata	3.131 (Unsexed)	-	-	-	-	-	Gulf of Mannar	Somavanshi (1989)
	2.8388 (F) 2.6872 (M)	-	20.0	October-March	-	1,50,000-2,00,000	Arabian Sea; Indian waters	Premalatha and Manojkumar (1990)
	2.3815 (Unsexed)	-	18.0	March-July	-	30,000-1,00,000;	Thoothukudi waters, Gulf of Mannar	Kasim and Balasubramanian, (1990); Kasim (2000)
	2.722 (M) 2.621(F)	1:0.86	31.26 (F) 31.12 (M)	September -February	3.51	20,520-2,22,422	Pamban Island waters, Gulf of Mannar	Vinothkumar *et al.* (2022(a) Vinothkumar *et al.* (2022(b))
Sphyraena jello	2.7587 (F) 2.6369 (M)	0.79:1; 1.06:1	-	April-July	4.0	3,00,000-5,00,000	Arabian Sea; Indian waters;	Premalatha and Manojkumar (1990)
	2.6229	-	-	July-September	-	-	Thoothukudi waters, Gulf of Mannar	Kasim (2000)
	2.87 (F) 2.77 (M)	-	-	April-June	-	-	Persian Gulf	Hosseini *et al.* (2009)
Sphyraena novaehollandiae	3.13 (F) 3.21 (M)	1.6:1	40.0 (M) 42.0 (F)	November-January	6.6	40,000-5,00,000	South Australia	Bertoni (1994)
Sphyraena putnamae	2.70 (F) 2.64 (M)	1.08:1	39.4 (F) 38.0 (M)	April-May & November-January	5.83	69,689-9,44,793	Karnataka waters, Arabian Sea	Rajesh *et al.* (2020)
	2.678(F) 2.794 (M)	1.49:1	41.3 (F) 40.6 (M)	September-October and April -June	5.11	51,507-1,063,438	Andhra Pradesh waters, Bay of Bengal	Ghosh *et al.* (2021)
	2.743 (F) 2.659 (M)	-	-	-	-	-	Pamban Island waters, Gulf of Mannar	Vinothkumar *et al.* (2022)
Sphyraena guachancho	2.5761	0.98:1	30.3 (F) 27.8 (M)	January	4.35	-	Ivorian coast	Akadje *et al.* (2019)
Sphyraena sphyraena	2.9094	1.12:1	27.6 (F) 26.7 (M)	April-August	10.0	46,778-1,03,453	Alexandria coast, Egypt	Allam *et al.* (2004)
Sphyraena barracuda	2.847; 2.967	1.6:1; 1.7:1	58.0 (F) 46.0 (M)	March-September	-	5,60,000-6,70,000	Indian Ocean; Florida Bay	DeSylva (1963); Kadison *et al*. (2010)
Sphyraena ensis	2.814 (F) 2.829 (M)	1.87:1	-	April-June	2.08	-	Gulf of California	Zavala-Leal *et al.* (2018)
Sphyraena idiastes	3.1918	2.0:1	-	-	-	-	Gulf of California	Gonzalez-Acosta *et al*. (2015)

The overall sex ratio observed (F:M) in the present study was 1.22:1, indicating the dominance of males. The domination of females in the population has been documented earlier by Avsar (1998) who reported that in a typical population, the male to female ratio will vary between 1:1 and 1:1.3. Similarly, a higher proportion of females has been reported for *S. putnamae* in Karnataka (Rajesh *et al*., 2020a) and Andhra Pradesh (Ghosh *et al*., 2021a). Similar dominance of females for barracudas in general has been reported globally (Table 2). The earlier studies found that variations in sex ratio in barracuda may be attributed to the aggregation of sexes for feeding, breeding and pre-spawning migration of males (De Sylva, 1963, 1973).

The smallest mature female and male were recorded at 12.5 and 16.5 cm FL, respectively. Length at first maturity for females and males was estimated at 55.30 and 45.4 cm FL (Fig. 4). The maximum proportion of mature female individuals was observed in the size class of 52.0-61.0 cm and 42.0-51.0 cm for males (Fig. 5). The estimated length at first maturity for the females was higher than the earlier reports from Karnataka (Rajesh *et al*., 2020a) and Andhra Pradesh (Ghosh *et al*., 2021) (Table 2). In the present

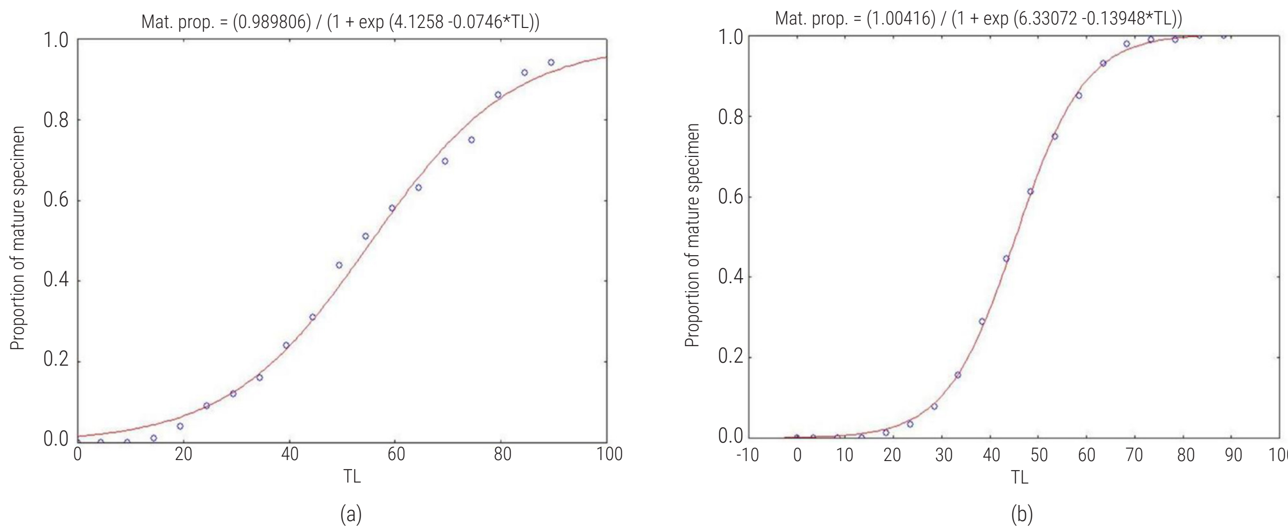

Fig. 4. (a) Length (FL) at maturity (L_{m50}) of female *S. putnamae;* (b) Length (FL) at maturity (L_{m50}) of male *S. putnamae*

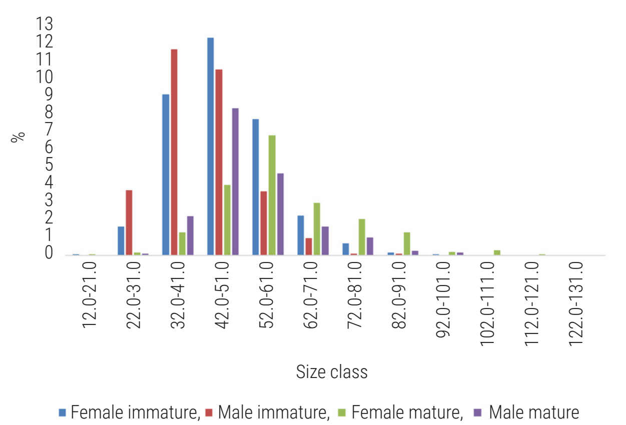

Fig. 5. Comparison of immature and mature size proportions between male and female *S. putnamae*

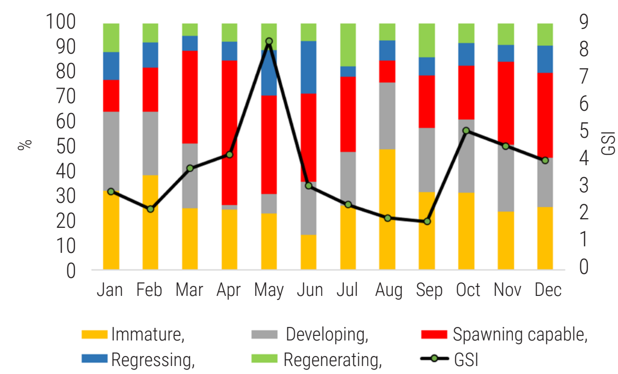

Fig. 6. GSI and relative frequency of maturity phases of female *S. putnamae*

pan-India study, a lower length at first maturity was observed for males which are similar to that reported for different barracuda species from global waters (Table 2). The significant variations in length at first maturity for fish species with respect to coasts may be attributed to factors such as food availability, migration, growth rate, longevity, and environmental conditions (*e.g.*, temperature changes) (Sabrah *et al*., 2018). Another important phenomenon is the allocation of more energy by the females towards reproductive development, resulting in a prolonged time required for maturation (Miller and Kendall, 2009). The length at first maturity for *S. putnamae* females was 55.30 cm which is much higher than the mean length estimated.

The monthly analysis of maturity phases of *S. putnamae* revealed that the 'spawning capable' females occurred almost throughout the year (Fig. 6). A higher proportion of 'spawning capable' females was observed from March to May, followed by November and December. GSI varied between 1.78 and 8.35 (Mean±SE;3.68±0.39) with peaks during March and November (Table 1). The higher proportion of spawning capable individuals and higher GSI values in females were recorded from March to May, followed by November and December which represents peak spawning periods for this species. However, other reproductive phases (Regressing, Regenerating) and moderate GSI values observed in the remaining months indicate that this species has extended spawning throughout the year (Fig. 6). Reports globally have indicated that barracudas have a single extended reproductive season (Table 2).

However, Pillai and Mahadevan (1981) have observed that ovarian development in barracudas is suggestive that the fish spawns more than once a year along the south-west coast of India. Similar such reports with bimodal spawning behaviour for *S. putnamae* have been reported from Karnataka and Andhra Pradesh waters by Rajesh *et al*. (2020a) and Ghosh *et al*. (2021a). In general, higher values of GSI synchronised with the maximum occurrence of spawning capable female individuals and it was evident from the monthly variation in the GSI values of females with a peak during March and November (Fig. 5). Further, the presence of other reproductive phases like spawning capable, regressing and regenerating with average GSI values for the remaining months confirmed that this species exhibits protracted spawning behaviour throughout the year like other tropical fishes. In the present study, the peak spawning activity was observed during the pre-monsoon summer season (April and May) with a minor one during the north-east monsoon (November and December) which indicates that environmental cues play an important role in the reproduction cycle of this fish. A similar phenomenon was also reported for *S. barracuda* by De Sylva (1963). Rajesh *et al*. (2020a) confirmed that the intensity of spawning in *S. putnamae* off Karnataka waters is regulated by the seasonal changes in temperature, salinity, and photoperiod similar to that reported for *S. putnamae* along Andhra Pradesh (Ghosh *et al*., 2021a). This result is comparable with the other reports made on barracudas from different coasts (Table 2).

Absolute fecundity ranged from 70,080 to 10,18,068 oocytes (Mean±SE=3,16,568±28,368 oocytes) and relative fecundity (oocytes g^{-1}) from 274 to 1,108 (Mean±SE= 679±2.3). Absolute fecundity correlated positively with fork length (R^2= 0.83) (Fig. 7a) and body weight (R^2=0.81) (Fig. 7b) indicating that larger females produce more eggs compared to smaller ones. Several groups of developing oocytes ranging in size from 0.11 to 0.90 (0.37±0.025 mm) were observed in the ripe ovaries of spawning capable females.

An earlier report from Andhra Pradesh waters showed a maximum absolute fecundity of 10,63,438 oocytes from a female of 103.8 cm FL and weighing 5,074 g (Ghosh *et al*., 2021a). Rajesh *et al.* (2020a) reported absolute fecundity of 9,44,793 oocytes from a female measuring 73.0 cm FL from Karnataka waters. In the present study, a higher relative fecundity (oocytes g^{-1}) ranging between 274 and 1,108 (Mean±SE = 679±2.3) was estimated, which was higher as compared to 285-964 g^{-1} oocytes reported by Rajesh *et al*. (2020a) and 192.79 to 518.17 g^{-1} oocytes as per Ghosh *et al*. (2021a). It is evident that *S. putnamae* has higher absolute fecundity as compared to other *Sphyraena* species (Table 2).

Studies on the food and feeding biology of a finfish give an idea about its feeding behaviour and its position in the food chain. Of the 2,135 individuals (1,023 females, 1,112 males) analysed, 75.97% (N=1,622) had either empty stomachs or stomachs with trace amounts of food, 15.27% (N=326) had part-full stomachs and 8.76% (N=187) had full stomachs. The estimated stomach vacuity index was 49.09% in females and 47.92% in males. In both sexes, 6.28 and 5.90% of individuals had part-full stomachs, whereas 3.61 and 5.29% of individuals had full stomachs. The stomach vacuity index and fullness index for different months of this species are depicted in Fig. 8. The highest feeding intensity was observed in October (14.08%) and September (13.15%). The lowest feeding intensity was observed during July (1.17%) and June (3.28%).

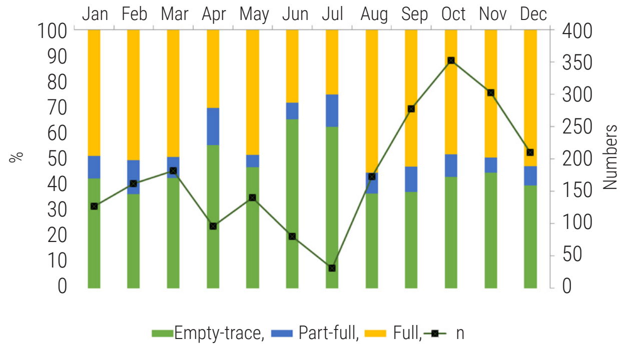

Fig. 8. Seasonal feeding intensity of *S. putnamae* (Stomach vacuity and Fullness index)

Barracudas are known for their voracious predatory behaviour. The elongated, protruding strong jaws with sharp teeth are used to pierce and predate the larger-sized live prey much bigger than their gape jaws (Habegger *et al*., 2010). Stomach vacuity was 75.9% in this study, which was significantly greater than previous reports from different coastal waters for *S. putnamae*. It was 47.3% in the north Persian Gulf waters (Mohammadizadeh *et al*., 2010), 40.42% in Karnataka waters (Rajesh *et al*., 2021b), and 54.76% in Andhra Pradesh waters (Ghosh *et al*., 2021b).

Globally, the larger barracuda species such as *S. barracuda*, *S. guachancho* and *S. chrysotaenia*, recorded higher stomach vacuity, which ranged between 56.0 and 63.0% (Schmidt, 1989; Ragheb, 2003; Akadje *et al*., 2013; Osman *et al*., 2019); whereas, the smaller barracuda species like *S. ensis*, *S. sphyraena*, *S. viridensis* and *S. flavicauda*, had a lower range of stomach vacuity, ranging from 14.0 to 40.8% as reported from different coastal regions (Barreiros *et al*., 2002; Ragheb, 2003; Kalogirou *et al*., 2012; Moreno-Sanchez *et al*., 2019; Osman *et al*., 2019). Arrington *et al*. (2002) mentioned that higher values of stomach vacuity in fishes could be attributed to the physiological disturbance in relation to the mode of exploitation. In general, more numbers of empty stomachs are observed in highly carnivorous fishes and could be due to stress caused during the retention of fish caught in the cod end for a long-time, leading to the regurgitation of prey due to contraction of esophageal muscles. The above-mentioned phenomenon is applicable in the present study as most of the samples were collected from the trawl landings. The lowest feeding intensity was

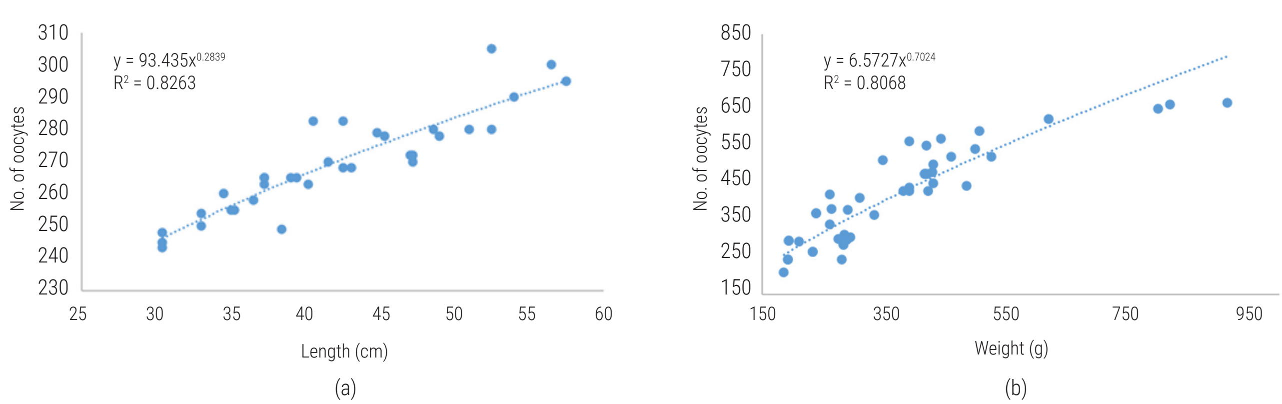

Fig. 7. (a). Relationship between fecundity to fork length of *S. putnamae* and (b). Relationship between fecundity to body weight of *S. putnamae*

observed during March, April, May and December which coincided with the peak spawning season for this species.

A similar observation with reduced feeding intensity during peak spawning season has been reported by Premalatha and Manojkumar (1990), Bertoni (1994), Ragheb (2003), Hosseini *et al*. (2009) and Osman *et al*. (2019) in *S. jello*, *S. obtusata*, *S. novaehollandiae*, *S. chrysotaenia* and *S. flavicauda*, respectively. Peak feeding intensity was observed during October and high feeding activity during September and November, perhaps correlated with reproductive seasons which may be attributed to the energy reserved for maturation of gonads when feeding activity reaches its peak. The stomach contents of *S. putnamae* contained 59 different prey items and they were classified into three major groups. Based on dietary coefficient (%QI). The dominant and preferred food item of *S. putnamae* was teleost (%QI=86.36; %IRI=82.40), followed by molluscs (%QI=7.76; %IRI=9.05) and crustaceans (%QI=5.87; %IRI=8.90), which were grouped as the secondary and accessory food items, respectively (Table 3). The teleosts consisted of 47 genera and 31 families. The primary prey constituents based on their dominance were Carangids, Clupeids, Engraulids and Scombrids. The most dominant teleost prey species observed were *Decapterus* spp. (22.90%), *Rastrelliger* spp. (13.74%) and *Stolephorus* spp. (11.07%), all belonging to pelagic groups. The less dominant teleost prey groups include *Megalaspsis cordyla* (3.79%), *Sardinella longiceps* (2.86%) and *Leiognathus* spp. (2.38%) (Table 3). In addition, part of the teleosts (%IRI=19.59) in the diets were in an advanced stage of digestion, hence could not be identified.

Trace amounts (0.15%) of the *Sphyraena* genus observed in the diet indicates the cannibalistic nature of the fish. The mollusc prey items belonged to the Loliginidae and Sepidae families, represented by *Loligo* spp. (7.60%) as the dominant one followed by *Sepia* spp. and *Sepiotetuthis* spp. A small number of unidentified squids in an advanced state of digestion (%IRI=0.44) also contributed to the diet. The crustacean group in the diet consisted of Sergestidae, Penaeidae and Squillidae. *Acetes* spp. (%IRI=7.09) was the dominant shrimp in the diet followed by unidentified shrimps (1.81%) and other shrimp genera formed less than 0.0029% in the diet.

The observation from the present study justified the fact that teleosts are the preferred and dominant diet item for *S. putnamae*. Teleosts contributed more than 86% of the diet component. This also substantiated the fact that similar to other tropical large pelagic species, *S. putnamae* also has a piscivorous feeding behaviour, followed by mollusc and crustacean components as secondary prey items. The piscivorous feeding preference of *S. putnamae* has been reported from the Western Pacific (Carpenter *et al*., 1997), Persian Gulf waters (Mohammadizadeh *et al*., 2010) as well as off Karnataka and Andhra Pradesh from India (Rajesh *et al*., 2021b; Ghosh *et al*., 2021b).

The preferred diet items of *S. putnamae* observed during the present study were carangids, clupeids, engraulids and scombrids. Similar reports through earlier studies by other researchers have indicated the presence of Indian mackerel, whitebait, Indian oil sardine, scads and silver bellies in the diet from the Persian Gulf (Mohammadizadeh *et al*., 2010). Rajesh *et al*. (2021b) reported carangids, scombrids, engraulids, silver bellies and synodontids as a major diet of the species based on samples from Karnataka coast and Ghosh *et al*. (2021b) reported the major diet of *S. putnamae* as sardines, whitebait, squid, bigeye scad, Indian scad, silver bellies and Indian mackerel from Andhra Pradesh coast.

Earlier works by different researchers on different species of barracudas also revealed the piscivorous feeding behaviour of barracudas with heterogeneous groups of diet components. *S. obtusata* predates on whitebaits, sardines and scads; *S. jello* on Indian mackerel, horse mackerel, scads, lizardfish and cuttlefish; *S. guachancho* on clupeids, sphyraenids, carangids and engraulids; *S. ensis* predate on species of clupeids and hemiramphids; *S. sphyraena* and *S. viridensis* on species of clupeids, atherinids and sparids; *S. chrysotaenia* predate on breams, whitebait, horse mackerel, scads, lizardfishes and cephalopods; and *S. flavicauda* on whitebaits, penaeid shrimps and squids (Randall, 1967; Sinha, 1987; Premalatha and Manojkumar, 1990; Carpenter *et al*., 1997; Paterson, 2001; Carpenter and Niem 2001; Barreiros *et al*., 2002; Ragheb, 2003; Bachok *et al*., 2004; Porter and Motta, 2004; Dananjanie *et al*., 2009; Hosseini *et al*., 2009; Mohammadizadeh *et al*., 2010; Kalogirou *et al*., 2012; Akadje *et al*., 2013; Moreno-Sanchez *et al*., 2019; Osman *et al*., 2019). The molluscs (*Loligo* spp. 7.60%) was observed as a secondary diet component of *S. putnamae* (Anusha and Fleming, 2014). Barreiros *et al*. (2002) reported that barracuda prefer cephalopods over crustaceans.

In the present study, the cannibalistic nature of *S. putnamae* was confirmed by the presence of *Sphyraena* spp. (0.15%) in the diet. Akadje *et al*. (2013) reported that cannibalistic nature was observed to a lesser extent in *S. putnamae* than in *S. guachancho*. The present study showed that the most preferred diet of *S. putnamae* belongs to schooling epipelagic prey groups (carangids, sardines, Indian oil sardine, whitebaits, anchovies, mackerels, Indian scads, bigeye scad) in Indian waters which is in line with earlier reports (Ghosh *et al*., 2021b; Rajesh *et al*., 2021b) and therefore this species is placed as a surface water feeder, similar to some other barracuda species (Kalogirou *et al*., 2012; Moreno-Sanchez *et al*., 2019). The predation upon shoal-forming active swimmers like clupeids, engraulids, carangids and scombrids account for higher quantities in the diet and indicates that this species has an aggressive feeding behaviour of chasing the prey. According to Barreiros *et al*. (2002), predation in barracudas is most effective when several individuals form schools and attack pelagic school-forming prey.

The present study has provided precise information on the length composition, reproductive and feeding characteristics of the sawtooth barracuda, *S. putnamae*. The exploitation of *S. putnamae*, with a dominance of the females, having FL less than that of estimated length at first maturity may lead to growth overfishing and this requires appropriate interventions for the fishery to be maintained at sustainable levels. The macroscopic observation of gonads revealed that this species has a year-round spawning behaviour with bimodal spawning periodicity. Further detailed studies on the microscopic structure of gonad and oocyte development during different months are required to confirm the reproductive traits of this species, which will help in framing suitable management regimes for the sustainable fishery of this resource. Studies on trophic interrelationships and energy flow help to understand the ecological importance of this species which will help the fishery managers to manage the resource through ecosystem-based fishery management.

Table 3. Food composition of *S. putnamae* as percentage by frequency of occurrence (OI), by weight (Wt), by number (NI), dietary coefficient (QI) and index of relative importance (IRI) of prey

Diet items	%FO	% Wt	%NI	QI	%QI	IRI	%IRI
Teleosts	79.80	86.19	64.75	424.86	86.36	913.41	82.40
Carangidae							
Decapterus spp.	9.41	18.55	8.42	156.29	31.77	253.85	22.90
Megalopsis spp.	4.39	6.77	2.79	18.89	3.84	41.98	3.79
Alectis spp.	1.51	0.63	0.75	0.47	0.10	2.07	0.19
Selar spp.	0.88	1.46	0.45	0.65	0.13	1.67	0.15
Selaroides spp.	0.38	0.52	0.40	0.21	0.04	0.35	0.03
Alepes spp.	0.25	1.10	0.15	0.16	0.03	0.31	0.03
Caranx spp.	0.25	0.28	0.20	0.06	0.01	0.12	0.01
Scombridae							
Rastrelliger spp.	7.65	14.07	5.83	82.08	16.68	152.35	13.74
Scomberomorus spp.	0.25	0.56	0.10	0.06	0.01	0.17	0.02
Engraulidae							
Stolephorus spp.	7.78	6.15	9.62	59.19	12.03	122.70	11.07
Thryssa spp.	2.63	1.88	2.39	4.49	0.91	11.25	1.02
Encrasicholina	1.00	0.62	1.10	0.68	0.14	1.72	0.16
Clupeidae							
Sardinella longiceps	4.14	4.38	3.29	14.40	2.93	31.74	2.86
Sardinella spp.	2.26	1.91	1.55	2.96	0.60	7.81	0.70
Amblygaster spp.	0.25	0.14	0.20	0.03	0.01	0.09	0.01
Hilsa spp.	0.13	0.04	0.05	0.00	0.00	0.01	0.00
Leiognathidae							
Leiognathus spp.	4.27	2.93	5.78	12.00	2.44	26.41	2.38
Nemipteridae							
Nemiptereus spp.	2.26	2.23	2.04	4.55	0.93	9.65	0.87
Lactariidae							
Lactarius lactarius	2.26	2.19	1.79	3.92	0.80	8.99	0.81
Synodontidae							
Saurida spp.	1.88	2.06	1.69	3.50	0.71	7.07	0.64
Saurida undosquamis	0.13	0.18	0.05	0.01	0.00	0.03	0.00
Bregmacerotidae							
Bregmaceros mcclellandi	1.76	0.81	1.99	1.62	0.33	4.93	0.44
Platycephalidae							
Platycephalus sp.	1.51	1.60	1.05	1.67	0.34	3.98	0.36
Sciaenidae							
Nibea spp.	1.13	0.93	0.70	0.65	0.13	1.83	0.17
Pennahia spp.	0.13	0.06	0.05	0.00	0.00	0.01	0.00
Haemulidae							
Pomadasys spp.	1.00	0.94	0.55	0.52	0.11	1.50	0.13
Trichuridae							
Trichurus spp.	0.50	1.67	0.20	0.33	0.07	0.94	0.08
Cynoglossidae							
Cynoglossus spp.	0.75	0.33	0.30	0.10	0.02	0.48	0.04
Tetraodontidae							
Lagocephalus spp.	0.63	0.42	0.25	0.10	0.02	0.42	0.04
Priacanthidae							
Piracanthus spp.	0.38	0.59	0.35	0.21	0.04	0.35	0.03
Mugilidae							
Mugil spp.	0.38	0.36	0.30	0.11	0.02	0.25	0.02
Harpodontidae							
Harpodon nehereus	0.25	0.52	0.20	0.10	0.02	0.18	0.02
Exocoetidae							
Cheilopogon spp.	0.38	0.70	0.15	0.11	0.02	0.18	0.02

Mullidae							
Upeneus spp.	0.25	0.48	0.25	0.12	0.02	0.18	0.02
Sphyraenidae							
Sphyraena spp.	0.38	0.24	0.15	0.04	0.01	0.15	0.01
Myctophidae							
Diaphus spp.	0.25	0.26	0.25	0.06	0.01	0.13	0.01
Serranidae							
Epinephelus spp.	0.25	0.29	0.10	0.03	0.01	0.10	0.01
Pseudanthias spp.	0.13	0.04	0.15	0.01	0.00	0.02	0.00
Balistidae							
Balistoides spp.	0.25	0.22	0.10	0.02	0.00	0.08	0.01
Muraenesocidae							
Muraenesox spp.	0.13	0.35	0.05	0.02	0.00	0.05	0.00
Monacanthidae							
Aluterus spp.	0.25	0.05	0.10	0.01	0.00	0.04	0.00
Gerridae							
Gerres spp.	0.13	0.11	0.05	0.01	0.00	0.02	0.00
Sillaginidae							
Sillago spp.	0.13	0.10	0.05	0.01	0.00	0.02	0.00
Siganidae							
Siganus spp.	0.13	0.08	0.05	0.00	0.00	0.02	0.00
Ambassidae							
Ambasis spp.	0.13	0.00	0.10	0.00	0.00	0.01	0.00
Dussumieriidae							
Dussumieria spp.	0.13	0.04	0.05	0.00	0.00	0.01	0.00
Unidentified fish	14.55	6.35	8.57	54.44	11.07	217.21	19.59
Molluscs	13.68	11.18	9.12	38.18	7.76	100.32	9.05
Loliginidae							
Loligo spp.	7.78	6.64	5.93	33.27	6.76	84.21	7.60
Sepioteuthis lessoniana	2.51	2.38	1.10	2.61	0.53	8.72	0.79
Sepiidae							
Sepia spp.	1.38	1.00	0.85	0.85	0.17	2.56	0.23
Unidentified squids	2.01	1.16	1.25	1.45	0.29	4.84	0.44
Crustaceans	6.64	2.22	26.30	28.87	5.87	98.61	8.90
Sergestidae							
Acetes spp.	3.89	1.15	19.04	21.95	4.46	78.55	7.09
Penaeidae							
Metapenaeus spp.	0.13	0.06	0.20	0.01	0.00	0.03	0.00
Squillidae							
Squilla spp.	0.13	0.02	0.05	0.00	0.00	0.01	0.00
Unidentified shrimps	2.50	0.98	7.01	6.90	1.40	20.01	1.81

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