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Original Article

Reproductive biology of 58 fish species around La Réunion Island (Western Indian Ocean): first sexual maturity and spawning period

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ABSTRACT

Background: The biological information of fish, which include reproduction, is the prerequisite and the basis for the assessment of fisheries.

Methods: The aim of this work was to know the reproductive biology with the first sexual maturity (TL_{50}) and the spawning period for 58 mainly fish species in the waters around La Réunion Island (Western Indian Ocean). Twenty families belonging to the Actinopterygii were represented (acanthuridae, berycidae, bramidae, carangidae, cirrhitidae, gempylidae, holocentridae, kyphosidae, labridae, lethrinidae, lutjanidae, malacanthidae, monacanthidae, mullidae, polymixiidae, pomacentridae, scaridae, scorpaenidae, serranidae, sparidae; 56 species; n = 9,751) and two families belonging to the Elasmobranchii (squalidae, centrophoridae; 2 species; n = 781) were sampled. Between 2014 and 2022, 10,532 individuals were sampled covering the maximum months number to follow the reproduction periods of these species.

Results: TL_{50} for the males and the females, respectively, ranged from 103.9 cm (*Acanthurus triostegus*) to 1,119.3 cm (*Thyrsitoides marleyi*) and from 111.7 cm (*A. triostegus*) to 613.1 cm (*Centrophorus moluccensis*). The reproduction period could be very different between the species from the very tight peak to a large peak covered all months.

Conclusions: Most species breed between October and March but it was not the trend for all species around La Réunion Island.

Keywords: gonad observation, reproduction period, reproductive maturity stages, size at the first sexual maturity

INTRODUCTION

The biological parameters (i.e. growth and reproduction) are essentially to management the fish population (Jakobsen et al., 2009). Fish reproductive biology is the necessary step to evaluate the reference points as spawning stock biomass and the maturity ogive, which are integrated in the stock assessment models (Jakobsen et al., 2009). The lack or scarcity of these biological information, can lead to over-exploitation of fisheries resources.

The main commercial demersal tropical fishes, along with snappers (Lutjanidae), groupers (Serranidae), emperors (Lethrinidae), carangids (Carangidae), soldierfishes (Holocentridae) and goatfishes (Mullidae) support locally important artisanal fisheries throughout the Indo-Pacific region, but quantitative assessments of these species have been limited by a lack of adequate biological and fisheries data (Newman et al., 2016; Halim et al., 2020), including around La Réunion Island (Le Manach et al., 2015). Among 123 fish species followed around La Réunion Island (Roos et al., 2022), The main objective of this study was to provide the reproductive biology information with the first sexual maturity and the spawning period for 58 mainly fish species required for the management of fisheries resources.

MATERIALS AND METHODS

Sampling

All fish sampled during scientific surveys, and some specimen were added from commercial landings to complete the length range or the months without surveys. During eight years (i.e. between 2014 and 2022), 10,532 individuals of 58 species were sampled. Twenty families belonging to the Actinopterygii were represented (acanthuridae, berycidae, bramidae, carangidae, cirrhitidae, gempylidae, holocentridae, kyphosidae, labridae, lethrinidae, lutjanidae, malacanthidae, monacanthidae, mullidae, polymixiidae, pomacentridae, scaridae, scorpaenidae, serranidae, sparidae; 56 species; n = 9,751) and two families belonging to the Elasmobranchii (squalidae, centrophoridae; 2 species; n = 781) were sampled (Table 1). All individuals were taken to the laboratory for accurate measurements. Each individual was measured to the nearest mm for total length (*TL*) and weighted to the grams for Total Weight (*W*). The gonads were observed macroscopically to determine the sex and this associated sexual maturity stage.

First sexual maturity

Sex ratios as the percentage of females (F) in the samples, were calculated. The first sexual maturity, to separate juveniles and sexually mature individuals thus defining the spawning biomass (i.e. reference point for exploited marine fishes) (Thorson et al., 2012), was measured from TL_{50}. This biological parameter was the total length at which 50% of individuals are mature for the first time.

Where m(*l*) is the proportion of mature individuals in

$$m(l) = exp^{(-exp^{-(a+b*l)})} \quad (1)$$

$$TL_{50} = \frac{-\ln(-\ln(0.5))-a}{b} \quad (2)$$

each length class (%), *a* is intercept, *b* is slope, *l* is the fish total length (cm) and TL_{50} is the mean total length at sexual maturity (50%, cm), were used. Among the Actinopterygii, two families (serranidae and lethrinidae, 13 species; Table 1) showed the protogynous hermaphrodites (i.e. change sex from female to male). For these species, first sexual maturity was only estimated for females.

Reproduction period

Fish were assigned to the following maturity development stages as recommended at the international level (ICES, 2018): from (I) immature; (II) resting; (III) ripe and running; (IV) spent; to (V) post-spent. From the percentage of individuals per month and per maturity stages throughout the year, the reproduction period and intensity were identified. The adults are the sum of all fish of maturity stages III, IV and V.

Statistical analysis

Statistical analyses to identify the significant sex effect on the first sexual maturity (with significant effect at $p < 0.05$) were carried out from the CAR package (Fox and Weisberg, 2011). This sexual dimorphism was tested on all fish species without two protogynous hermaphrodites families. The figures were carried out from the ggplot2 (Wickham, 2016) and plyr (Wickham, 2011) packages in the R statistical environment (R Core Team, 2023).

Ethical statement

All species were sampled from scientific surveys or caught for the commercial landings. They are not in the IUCN red list as critically endangered, endangered or vulnerable species.

RESULTS

Among 10,532 individuals, there were 4,271 males, 5,346 females and 915 immatures. Summarised informa-

Table 1. Sampling details (number and length by sex: males, M; females, F and immatures, I) with the first sexual maturity (TL_{50}; p-value < 0.05 showed the significant sexual dimorphism) for 58 species around La Réunion Island (*protogynous hermaphroditism species)

Famille	Latin mame	Number				Length of adults (F+M)			Length of Males			Length of Females			TL_{50}			
		Total	Males	Fe-males	Imma-tures	Mean	SD	Range (min-max)	Mean	SD	Range (min-max)	Mean	SD	Range (min-max)	Males	Fe-males	Adultes (F+M)	p-value
Acanthuridae	*Acanthurus triostegus*	542	214	225	103	152.0	21.3	34-199	154.6	18.0	99-199	150.7	16.4	95-192	103.91	111.68	108.30	0.21
	Naso elegans	63	40	18	5	322.7	86.6	167-469	336.1	77.3	208-459	266.1	86.0	167-426		214.39	204.65	
	Naso unicornis	176	98	67	11	299.6	94.9	157-557	322.8	93.4	167-557	266.5	91.8	157-532	247.76	209.43	231.65	< 0.05
Berycidae	*Beryx decadactylus*	49	20	27	2	503.1	67.6	350-610	458.9	57.2	350-550	528.9	58.9	388-610				
Bramidae	*Eumegistus illustris*	236	96	127	13	680.6	135.1	452-1,000	661.3	126.0	470-910	692.8	142.2	452-1,000	628.56	521.05	575.55	0.09
Carangidae	*Caranx melampygus*	65	45	20	0	609.1	96.0	433-838	621.1	100.2	467-838	582.0	81.9	433-710				
	Decapterus tabl	63	23	29	11	266.9	26.0	193-326	267.0	23.7	233-313	264.6	29.9	193-326		215.05	215.06	
Centrophoridae	*Centrophorus moluccensis*	69	31	38	0	589.1	309.0	0-876	644.5	182.6	0-741	543.9	379.2	0-876	548.51	613.07	556.26	< 0.05
Cirrhitidae	*Cirrhitus pinnulatus*	69	42	24	3	189.5	22.1	140-252	196.8	18.0	168-252	177.3	23.5	140-223				
Gempylidae	*Promethichthys prometheus*	86	28	53	5	381.1	77.0	216-564	356.0	68.3	263-490	401.8	73.4	282-564	386.05	356.92	361.93	< 0.05
	Rexea prometheoides	135	16	115	4	298.6	50.8	0-425	257.4	21.1	222-320	306.7	43.0	0-425				
	Thyrsitoides marleyi	36	9	24	3	1,092.4	463.0	222-1,890	1,009.8	342.0	410-1,280	1,223.3	426.0	320-1,890	1,119.30			
Holocentridae	*Myripristis berndti*	122	60	55	7	233.3	43.4	126-308	239.8	42.2	126-308	229.9	42.4	127-292	129.96			
	Myripristis chryseres	87	48	37	2	206.1	20.2	150-255	215.9	18.1	182-255	194.8	15.5	150-215		155.99	159.95	
	Myripristis murdjan	73	23	46	4	200.5	29.5	145-255	198.2	25.1	145-234	205.4	30.0	146-255				
	Ostichthys kaianus	40	16	21	3	283.2	43.7	165-360	291.0	43.4	188-360	282.8	38.4	184-344				
	Sargocentron spiniferum	38	13	22	3	268.2	52.1	181-371	275.8	50.0	220-361	268.4	54.3	196-371		210.31	212.85	
Kyphosidae	*Kyphosus bigibbus*	27	14	12	1	317.4	27.6	244-365	326.1	16.9	296-353	308.7	35.4	244-365		289.89	287.68	
	Kyphosus cinerascens	32	19	13	0	327.6	63.0	205-470	305.8	48.7	205-360	359.3	69.7	271-470	241.23		240.18	
	Kyphosus vaigiensis	25	17	7	1	306.7	49.4	203-395	292.9	48.9	203-395	347.0	23.5	304-375				
Labridae	*Cheilinus trilobatus*	79	13	56	10	314.1	76.9	184-477	355.5	73.9	184-473	305.1	77.0	200-477				
Lethrinidae	*Gnathodentex aureolineatus**	60	13	38	9	234.3	37.2	155-303	241.9	27.8	182-273	241.6	34.8	173-303		187.70	187.70	
	*Lethrinus rubrioperculatus**	125	36	87	2	339.6	66.5	192-464	401.1	17.5	354-433	315.1	61.7	194-464		208.62	208.62	

Table 1. Continued

Famille	Latin mame	Number				Length of adults (F+M)			Length of Males			Length of Females			TL_{50}			
		Total	Males	Fe-males	Imma-tures	Mean	SD	Range (min-max)	Mean	SD	Range (min-max)	Mean	SD	Range (min-max)	Males	Fe-males	Adultes (F+M)	*p*-value
Lutjanidae	*Aphareus rutilans*	162	90	64	8	429.8	91.4	211-786	429.5	92.5	211-786	434.4	92.6	319-769	353.70	381.76	368.81	< 0.05
	Aprion virescens	65	40	24	1	443.1	123.2	212-893	427.3	106.2	288-670	477.5	137.2	323-893	324.04		320.30	
	Etelis carbunculus	1,700	881	777	42	277.1	70.9	139-1,250	270.6	59.3	164-980	286.7	81.4	153-1,250	183.95	183.46	188.18	0.87
	Etelis coruscans	193	85	98	10	455.6	249.2	206-1,155	450.6	240.2	206-1,068	480.0	268.1	220-1,155	391.99	394.25	397.49	0.83
	Lutjanus bengalensis	25	6	19	0	177.2	19.3	147-217	166.5	14.3	147-189	180.6	19.7	152-217				
	Lutjanus kasmira	753	360	373	20	219.6	34.9	110-336	230.1	37.1	150-336	211.2	28.9	110-281	180.22	147.11	161.29	< 0.05
	Lutjanus notatus	397	201	195	1	215.2	22.8	143-277	224.3	22.3	155-277	206.2	19.0	143-247				
	Pristipomoides argyrogrammicus	647	317	317	13	232.2	31.8	122-317	239.4	31.3	162-316	226.8	29.6	140-317		148.06	149.34	
	Pristipomoides filamentosus	300	98	171	31	262.8	51.1	155-576	273.3	61.1	157-576	264.4	42.3	165-383	326.90	310.35	317.37	0.18
	Pristipomoides multidens	270	140	129	1	501.8	128.3	270-865	514.9	132.0	282-865	487.6	123.0	270-815	388.63	346.15	369.62	< 0.05
Malacanthidae	*Branchiostegus doliatus*	33	16	15	2	342.7	42.9	247-422	356.1	36.2	303-422	326.7	48.0	247-410				
Monacanthidae	*Cantherhines dumerilii*	56	25	25	6	279.9	35.2	185-355	274.4	27.6	185-312	292.8	38.5	233-355	240.00		219.39	
Mullidae	*Mulloidichthys flavolineatus*	421	45	45	331	137.9	64.2	85-415	197.1	79.4	95-319	242.5	86.5	97-415	185.17	204.51	207.04	0.37
	Mulloidichthys pfluegeri	58	26	31	1	332.5	58.4	193-452	339.0	50.4	215-429	328.7	65.1	193-452	259.33	240.43	247.93	0.61
	Parupeneus trifasciatus	269	98	113	58	226.1	55.6	79-401	255.7	61.7	141-401	213.1	37.3	129-352	218.90	199.22	212.92	0.63
Polymixiidae	*Polymixia berndti*	72	17	46	9	230.4	63.8	151-430	248.2	89.2	151-430	226.0	57.7	160-429				
	Polydactylus sexfilis	107	49	25	33	309.3	148.8	70-519	379.6	30.5	311-457	440.8	35.5	366-519			256.55	
Pomacentridae	*Abudefduf septemfasciatus*	27	20	6	1	206.2	11.3	180-227	203.9	11.8	180-227	213.8	6.4	207-224				
Scaridae	*Calotomus carolinus*	67	26	39	2	354.5	55.3	186-456	384.0	55.4	202-456	334.0	47.4	186-403	245.72	240.00	240.00	0.81
	Chlorurus enneacanthus	168	72	87	9	321.4	84.1	175-765	333.1	89.5	175-765	312.1	80.8	182-560		209.58	200.53	
	Scarus psittacus	117	68	44	5	278.6	47.4	121-364	300.2	35.3	198-364	248.7	38.4	137-326		164.74	154.02	
Scorpaenidae	*Pontinus nigerimum*	37	12	15	10	275.6	51.8	161-380	311.3	28.6	273-370	241.9	47.1	161-298				

Table 1. Continued

Famille	Latin mame	Number				Length of adults (F+M)			Length of Males			Length of Females			TL_{50}			
		Total	Males	Fe–males	Imma–tures	Mean	SD	Range (min–max)	Mean	SD	Range (min–max)	Mean	SD	Range (min–max)	Males	Fe–males	Adultes (F+M)	*p*–value
Serranidae	*Cephalopholis aurantia**	222	54	155	13	228.5	35.8	136–318	259.9	25.2	219–318	220.4	32.3	136–313		160.39	160.39	
	*Cephalopholis nigripinnis**	31	10	20	1	167.4	27.4	119–230	178.8	23.3	145–209	162.1	28.8	119–230				
	*Cephalopholis spiloparaea**	47	20	27	0	170.0	24.9	129–236	176.8	25.3	134–236	165.0	23.9	129–230				
	*Epinephelus fasciatus**	301	33	264	4	230.7	54.2	100–421	273.9	66.3	164–421	225.8	50.1	100–353		130.28	130.28	
	*Epinephelus hexagonatus**	314	63	207	44	166.0	27.9	112–241	181.1	25.2	127–233	158.8	28.0	112–241				
	*Epinephelus merra**	134	16	107	11	181.1	29.0	120–254	188.1	28.2	149–230	180.3	29.9	120–254		166.20	166.20	
	*Epinephelus radiatus**	114	9	99	6	364.2	108.1	123–653	392.7	95.8	280–562	368.3	106.7	187–653		317.71	317.71	
	*Epinephelus tauvina**	72	22	38	12	267.7	67.7	158–518	256.9	70.5	187–518	285.2	65.1	158–450		268.72	268.72	
	*Gnathodentex aureolineatus**	60	13	38	9	234.3	37.2	155–303	241.9	27.8	182–273	241.6	34.8	173–303		187.70	187.70	
	*Variola albimarginata**	152	45	106	1	358.6	78.7	185–555	428.0	62.3	257–555	330.3	65.4	185–494		236.26	236.26	
	*Variola louti**	71	24	47	0	580.1	136.7	216–840	649.3	145.8	392–840	544.7	118.4	216–741		363.01	363.01	
Sparidae	*Argyrops filamentosus*	61	34	22	5	239.6	21.7	195–290	244.2	22.6	198–290	239.6	15.9	214–270				
Squalidae	*Squalus megalops*	712	302	397	13	512.0	190.2	0–820	460.2	187.6	0–683	559.8	171.4	0–820	397.67	500.00	454.63	< 0.05

tion for each species, by each sex or both males and females, is presented in Table 1 and Supplementary Table 1. Among 23 families, two were represented by a relatively high number of species, such as the Serranidae (11 species) and Lutjanidae (10 species). In the sameway, these two families showed the large number of individuals with 4,512 belonging to the Lutjanidae and 1,518 belonging to the Serranidae. According to the selected species, the distribution between the two sexes and the immatures can be very different. While the reproduction of protogynous hermaphrodites (i.e. for two families: serranidae and lethrinidae represented by 13 species) explained why males could be larger than females, for other species, there was no generalizable observable trend between males and females and it depends on the analysed species.

Among 58 analysed species, the mean total length of the first sexual maturity (TL_{50}) could be modelled from individual *in situ* data for 40 species (Table 1). TL_{50} for the males and the females, respectively, ranged from 103.9 cm (*Acanthurus triostegus*) to 1,119.3 cm (*Thyrsitoides marleyi*)

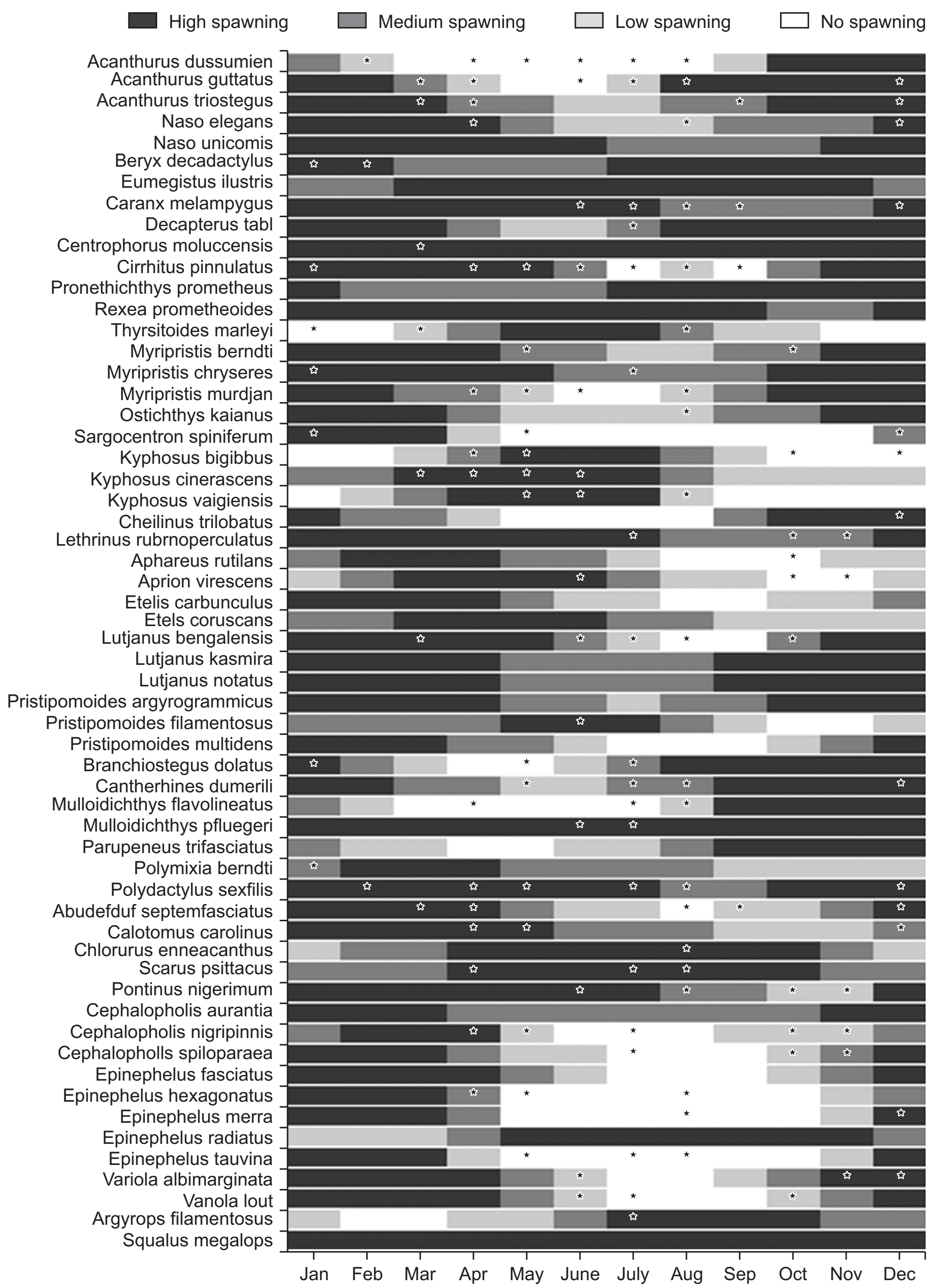

Fig. 1. Reproduction period and intensity (percentage of individuals actively breeding: No spawning: 0-25%; Low spawning: 25-50%; Medium spawning: 50-75%; High spawning: 75-100%) of species around La Réunion Island (*month without sampled individuals).

and from 111.7 cm (*A. triostegus*) to 613.1 cm (*Centrophorus moluccensis*) (Table 1). For ten hermaphrodites' species, only TL_{50} for females was modelled. For 30 other species presenting the TL_{50} fitted on the data, this biological parameter was measured for the males and for the females for 16 species. Among these species, 10 a higher TL_{50} for females than for males and only 6 have the opposite trend. The significant different of TL_{50} between the males and the females were observed for 7 species among 16 species (Table 1).

For all 58 species, the reproduction period and intensity were analysed for each species including all adults' individuals (Fig. 1) and by each sex (females Supplementary Fig. 1 and males Supplementary Fig. 2). There were three species including the two Elasmobranchii species (*Squalus megalops* and *Centrophorus moluccesis*) and one species of the mullidae family (*Mulloidichthys flavolineatus*) showed that the reproduction peak (i.e. high spawning period; Fig. 1) covered all months. Conversely, other species presented the reproduction peak very tightly spread over 3 months (*Thyrsitoides marleyi; Kyphosus bigibbus; Aphareus rutilans; Pristipomoides filamentosus; Polymixia berndti; Cephalopholis nigripinnis; Epinephelus hexagonatus*). However, for the species with the restricted reproduction period, most species breed between October and March but it was not the trend for all species. The reproduction activity may be concentrated in the winter months for a limited number of species as *Argyrops filamentosus, Pristipomoides filamentosus, Kyphosus vaigiensis* and *Kyphosus bigibbus* (Fig. 1).

DISCUSSION

Reproductive process through the sexual maturity and the peak of reproduction are important elements prerequisite to realize the stock assessment with a good precision (Chen et al., 2022). However, for many fish species, the females and males and their maturity stage cannot be distinguished by only external characteristics. Consequently, for many cases of study, this information is lack, very old or partial. Moreover, for tropical species as around La Réunion Island, there may be conservation problems due to the high temperature after fishing which result in difficulties in observation internal organs such as the gonads. Consequently, this type of study aggregating reproductive information from organ observations in the laboratory for a very large number of species is necessary to provide reference points for each species, which can be used in fisheries resource monitoring as is done for other biological parameters such as the length-weight relationship (Roos et al., 2022).

Firstly, the length of the first sexual maturity (TL_{50}) was measured for each species. Among fish species, there are two mainly sexual characteristics: hermaphrodites versus dioecious species. For the protogynous hermaphrodites, concerning two families (serranidae and lethrinidae, 13 species), the first sexual maturity of females is earlier than the sex change and consequently the length is not the same (Frisch et al., 2016). For the dioecious species, there are no clearly patterns between the TL_{50} for females and males. Some species show comparable TL_{50} between males and females, others show marked differences in favor of females or males. These differences between sexes within the same population or between several population in the length at the sexual maturity, can be caused by phenotypic changes, genetic adaptations or the interaction of both (Law, 2000; Trindade-Santos and Freire, 2015). TL_{50} is influenced by environmental conditions (Weatherley, 1990), but human activities could be the potential factors (i.e. fishing, pollution…). For example, a negative relationship between the length at sexual maturity and the level of fishing pressure was observed (ICES, 2012; Marty et al., 2014).

Secondly, the timing and intensity of the spawning were estimated for each species. For this reproductive trait, there are mainly difference among species with some species with a very large reproduction peak covered all months and conversely, others with very tight reproduction peak over 3 months. These results corroborate the same approach applied in the Mediterranean Sea (Tsikliras et al., 2010). Some species that breed strongly throughout the year may show two sexual strategies with some individuals breeding once a year and others at least twice (Bye, 1984; Cushing, 1990). The duration and the period of the year of the reproduction peak varies between the species and between the populations within the same species. The spawning season begin when the fish receive the environmental stimuli (Hoar, 1969; Liley, 1969). Lunar periodicity seems to be the influential external stimulus on reproductive characteristics of tropical coastal fish species (Harrison et al., 1984; Thresher, 1984). Another important factor to trigger the reproduction could be internal with the hormonal cascades leading to maturation and spawning and the gill surface area (Pankhurst, 2016; Pauly, 2019; Pauly, 2022). Finally, the reproduction biology could linked to the age class of the specimen with the ontogenic effect (Rijnsdorp, 1989; Trippel et al., 1997).

CONCLUSION

The reproductive biology information with the first sexual maturity and the spawning period were analyzed for 58 mainly fish species around the La Réunion Island in the Indian Ocean. For many species, these biological data were not available or were very old. The first sexual maturity length is essential to evaluate the reference point named the spawning stock biomass (SSB) (Thorson et al., 2012) used in the stock assessment and the reproduction period is important as proxy to explain the individuals movement (i.e. during reproduction period, the fish gather in groups) and/or to define temporal management rules. All biological data can be used in the future for natural resource management, which allows sustainable fishing. Moreover, another complementary analysis of the gonads through the histological approach could be realized in the future.

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SUPPLEMENTARY MATERIALS

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