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Age-Based Population Dynamics of the Shoemaker Spinefoot Rabbitfish (*Siganus sutor*) From the Seychelles

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ABSTRACT

Spawning aggregations, schooling behaviour and twice-yearly recruitment make the shoemaker spinefoot rabbitfish (*Siganus sutor*) a major artisanal and subsistence fishery species in the Western Indian Ocean. However, published estimates of its maximum age and growth parameters vary considerably. In this study, we estimate the longevity of *S. sutor* at 4 years and an asymptotic length of 287.29 mm FL. When analysed by sex, males exhibited a larger L_∞ (292.53 mm FL) than females (284.52 mm FL), yet likelihood-ratio tests and confidence ellipses formulated around L_∞ and K values indicated no significant sex-based differences in growth profiles. Consistent with previous studies, *S. sutor* is short-lived, grows rapidly and experiences high mortality yet remains resilient to fishing pressure. However, given its importance to coastal fisheries throughout the Indian Ocean, we recommend a comprehensive, spatially comparative assessment of *S. sutor* life-history traits and population dynamics across its geographic range. This is necessary to determine whether inconsistencies in age and growth reported in the literature are due to the presence of a species complex with differing growth rates, mortality, behaviour or vulnerability to fishing.

1 | Introduction

The shoemaker spinefoot rabbitfish, *Siganus sutor*, is endemic to the Western Indian Ocean (WIO) [1–3]. It is closely associated with a variety of coastal habitats, including coral reefs, tropical macroalgal beds, seagrass meadows [4] and mangroves and rocky reefs [5]. It has been characterised as a generalist herbivore that feeds predominantly on turf algae [6] but also exploits a wide range of trophic resources, including seagrass blades and epiphytes [7] and thallous macroalgae [8, 9].

S. sutor is one of the most popular fishery targets in the WIO, due to their schooling behaviour and predictable spawning aggregations [1, 2, 10–12]. It is widely exploited in coastal subsistence and artisanal fisheries along the East African coast and is among the most commonly landed species in Kenya, where it accounts for approximately 40% of artisanal fishery landings [12]. Despite its central importance to local fisheries, knowledge of its population dynamics remains limited, particularly with respect to age-based parameters that are essential for effective fisheries management.

S. sutor is a gonochoristic species with an extended spawning season lasting several months. Gonadal studies indicate at least two reproductive peaks per year across much of its range [13–17]. This near year-round reproductive activity, combined with multiple recruitment events [18], has led to the perception that *S. sutor* populations are relatively resilient to fishing pressure [1]. However, resilience may vary spatially and temporally, and

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assumptions of sustainability remain largely untested in many parts of its distribution.

To date, few studies have conducted comprehensive age- and growth-based population analyses of *S. sutor* across its geographic range, and existing estimates of key parameters such as growth rates and longevity vary widely (e.g., [18–20]). This study addresses this critical knowledge gap by providing detailed, sex-specific analysis of age structure, growth and population dynamics of *S. sutor* from the Seychelles. By improving our understanding of the species' life-history characteristics, this work contributes essential information for the sustainable management and conservation of reef fisheries that support tropical coastal communities.

2 | Materials and Methods

2.1 | Sample Collection

Samples were collected by commercial fishers around Praslin Island in the Seychelles (4.3326° S, 55.7467° E), using baited traps (locally known as 'kazye") with a minimum hexagonal mesh size of 40 mm. Fish specimens were acquired from these fishers between October 2013 and August 2014 and randomly selected for biological sampling. For each specimen, the fork length (FL) was measured to the nearest millimetre, and total weight was recorded to the nearest gram. Individuals were sexed macroscopically as male or female. Sagittal otoliths were extracted, cleaned with distilled water and stored dry for subsequent age analysis. In total, 144 specimens were collected.

2.2 | Age Estimation

Age estimation was based on thin transverse sections of sagittal otoliths [21, 22]. *S. sutor* otoliths were processed in batches and sectioned with a 9-μm UltraPrep metal-bonded diamond disc to reach an approximate thickness of 250–300 μm. The estimation of age was conducted by counting opaque growth rings from the core to the distal edge of each section. The annual periodicity of opaque zone formation in *S. sutor* has been previously validated through back-calculation [23]. Samples were observed under reflected light against a black background with magnification over 40× (Figure 1). Each sample was blind-read by at least two experienced readers, who independently assigned an age to each otolith. If both readers provided the same age estimate, that value was accepted as the final age. In cases where estimates differed, a consensus age was determined through a joint examination. Seventy-four males and 70 females were successfully aged.

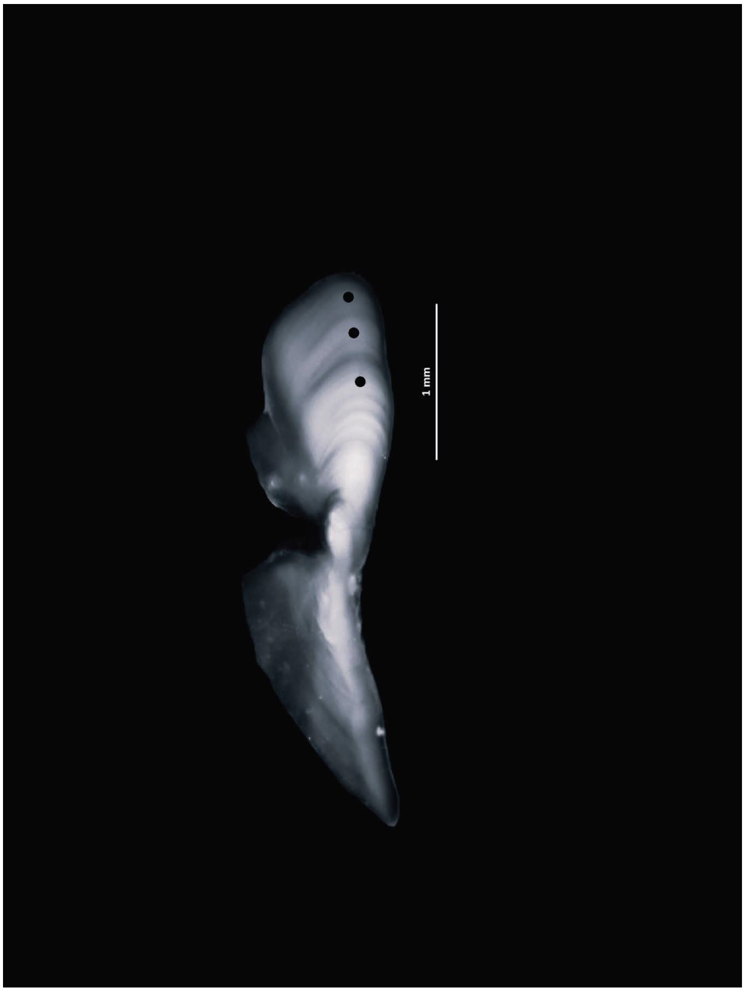

FIGURE 1 | Sectioned otolith of a 3-year old *Siganus sutor* viewed under a transmitted light. Distinctive opaque growth increments selected as annual rings are marked.

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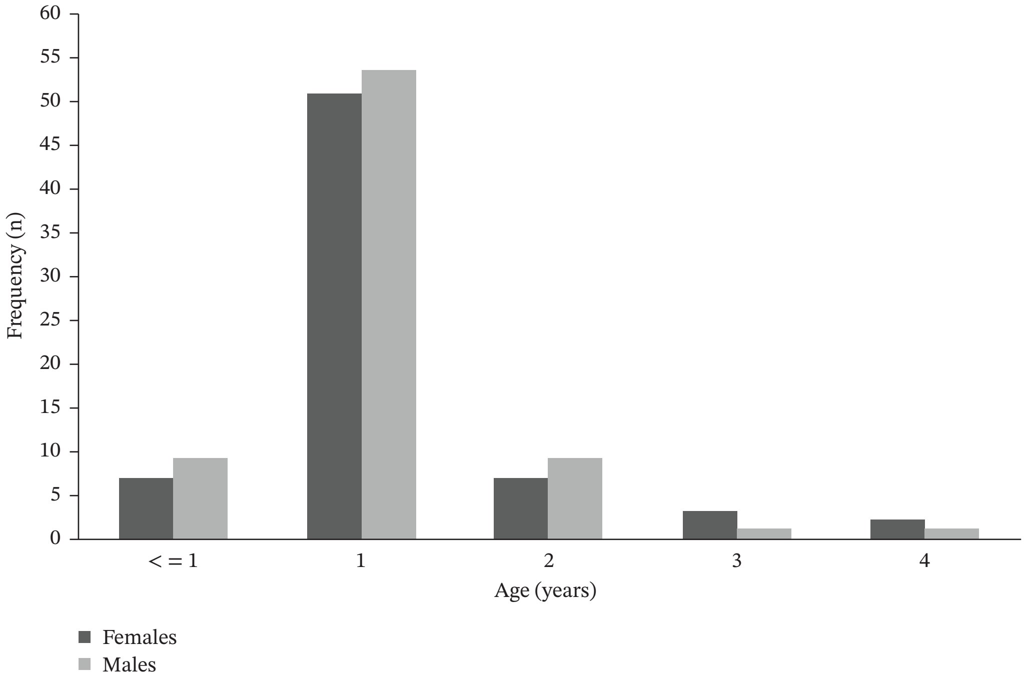

FIGURE 2 | Age distribution of male and female *Siganus sutor*.

2.3 | Population Parameters

Size and length distribution were plotted to examine the spread of growth and longevity for this species. Using the same age-based distribution, instantaneous total mortality (Z) for *S. sutor* was calculated. Mortality was calculated as $Z = 100 - S$, where S is the survivorship calculated as $S = \exp(-a)$, with a corresponding to the absolute value of the slope of the line ($y = ax + b$) [24, 25]. All age groups before the modal age class (i.e., age groups not fully recruited to the fishery) were excluded from the mortality regression analysis. The length–weight relationship of *S. sutor* was examined to determine whether the species exhibits isometric or allometric growth. This was described as $W = a \times L^b$ [26], where W represents the total weight (g), L is the total length (mm), a is the y-intercept or initial growth coefficient and b is the slope or growth coefficient. A b value of 3.0 indicates isometric growth, meaning weight and length increase at the same proportional rate. Values of b less than 3.0 reflect negative allometric growth, where fish grow proportionally more in length than weight. Conversely, a b value greater than 3.0 indicates positive allometric growth, with weight increasing at a proportionally higher rate than length. The von Bertalanffy growth function (VBGF) [27] was used to analyse the relationship between age and length. This was modelled using the formula $L(t) = L_\infty[1 - \exp^{-K(t-t0)}]$, where $L(t)$ is the average length of the fish at age t; L_∞ is the asymptotic length; K is the rate of growth toward the asymptotic length; and t_0 is the theoretical age at which the fish's length is zero. Based on size-at-settlement information for *S. sutor* (10 mm) reported by Ntiba and Jaccarini [19], we constrained the early portion of the growth curve to ensure that the VBGF passed through a biologically realistic starting point. Comparison of VBGF parameters between the sexes was conducted using likelihood ratio test (LRT) [27, 28]. We also compared growth between sexes by generating 95% confidence ellipses around the least-squares estimates of L_∞ and K [27, 28]. Nonoverlap between the confidence regions was taken as evidence of a significant difference in the growth parameters.

3 | Results

The age distribution of *S. sutor* ranged from 1 to 4 years (Figure 2), with 1-year-olds being the modal age class. Size distribution ranged from 185 mm to 345 mm (FL), with 210–229 mm size class being the most prevalent (Figure 3). Males and females were observed across all age and size classes, indicative of the gonochoric sexual development pathway in Siganids [4, 29]. The relationship between length and weight was negatively allometric, with b values less than 3, both overall and also partitioned by sex (see Table 1).

Mortality estimates calculated from age-based catch curves showed an annual survivorship rate of approximately 30% per year, which is expected from a short-lived species (see Table 1). The relationship between age and length was asymptotic. VBGF analysis (Figure 4) showed that *S. sutor* reaches an asymptotic length of 287.29 mm (FL), and when partitioned by sex, males reached a slightly bigger size (292.53 mm FL) compared to females (284.52 mm FL). However, the LRT revealed no significant difference in growth parameters between males and females ($p = 0.11$). This result was further supported by the confidence ellipses (Figure 5) formulated around values of L_∞ and K, which showed overlap between males and females, indicating no meaningful divergence in growth trajectory.

4 | Discussion

The *S. sutor* fishery has long been regarded as one of the most productive coastal fisheries in the Indian Ocean, largely owing to the species' biannual recruitment and extended reproductive season. This regular influx of recruits is thought to confer a degree of resilience to sustained fishing pressure. Nevertheless, despite its ecological and socioeconomic importance, *S. sutor* has not yet been the subject of a comprehensive, large-scale demographic assessment across its geographical range.

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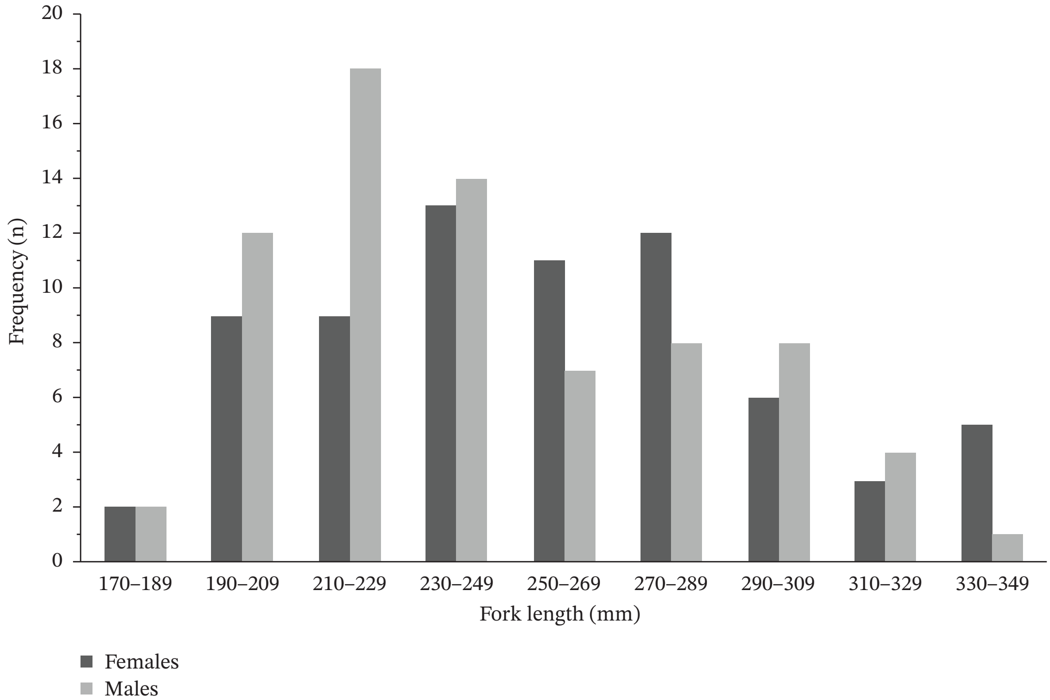

FIGURE 3 | Size distribution of male and female *Siganus sutor*.

TABLE 1 | Population parameter values of best-fit models for *Siganus sutor;* growth parameters of von Bertalanffy growth function (VBGF) showing sex-specific and overall growth trajectories, length–weight relationship fitted to a power curve, mortality estimates calculated from age-based catch curves and sex ratio.

Function	Parameters	*Siganus sutor*
VBGF (combined)	L_∞	(FL mm) 287.29
	K	2.02
	t_0	−0.01
VBGF (male)	$L\infty$	(FL mm) 292.53
	K	1.79
	t_0	−0.02
VBGF (female)	L_∞	(FL mm) 284.52
	K	2.26
	t_0	−0.02
Length–weight relationship	n	144
	b	2.91
	R^2	0.97
Length–weight relationship (male)	n	74
	b	2.93
	R^2	0.97
Length–weight relationship (female)	n	70
	b	2.87
	R^2	0.96
Morality (years^{-1}) -	Z (%)	70.044
Morality (male years^{-1})	Z (%)	75.74
Morality (female years^{-1})	Z (%)	65.23
Sex ratio	M:F	1.06:1

In the present study, we estimated a maximum longevity of 4 years based on a substantially larger sample size ($n = 144$) than most previous investigations. Earlier studies have reported a wide range of maximum ages, including approximately two years from daily increment counts of 45 otoliths [19], 3 years from an unspecified number of otolith readings [18], 1 year from length–frequency analysis of 82 specimens [20] and 5 years from increment counts of 41 otoliths [30]. While these studies differ in methodology and sampling intensity, they consistently indicate that *S. sutor* is a short-lived species with rapid turnover. Our estimate of 4 years lies toward the upper end of this range and likely reflects the sensitivity of longevity estimates to both methodological choices and sample composition, especially in short-lived species.

Our estimate of asymptotic length (287.29 mm FL) differs from previously published values, including 432.8 mm FL [20], 362 mm SL [19], 400 mm TL [18] and 386 mm TL [30]. While some of this variation reflects differences in length metrics (FL, SL and TL), it also underscores the possible influence of sampling design, such as fishing-gear selectivity.

Despite differences in absolute growth parameters among studies, there is strong agreement that *S. sutor* grows rapidly and reaches near-asymptotic size within the first year of life. Such rapid growth is typical of small-bodied reef fishes that experience high natural mortality and must quickly transition from vulnerable juvenile stages to reproductive adults [31]. For a schooling herbivore such as *S. sutor*, rapid growth may be particularly advantageous because individuals forage in exposed reef and seagrass habitats where predation risk is high. Achieving adult size quickly likely improves survival while enabling individuals to participate in spawning aggregations early in life. Our estimate of total mortality (0.7 years^{-1}) is comparable to that reported by Grandcourt [20] (0.63 years^{-1}), higher than the

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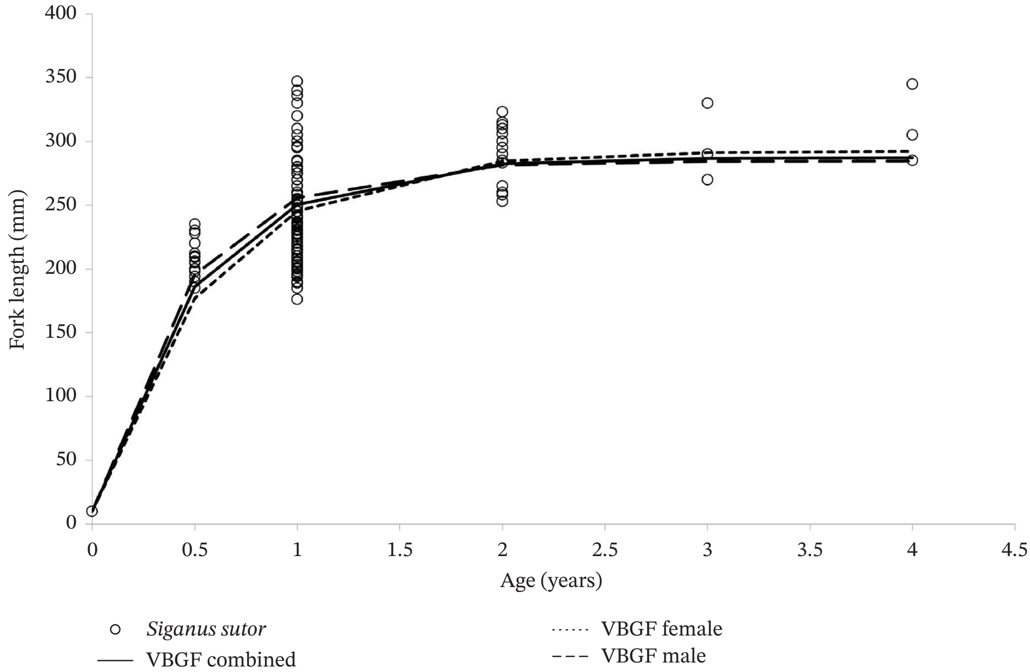

FIGURE 4 | Sex-specific von Bertalanffy growth trajectories of male and female *Siganus sutor*. Overall and sex-specific parameters are presented in Table 1.

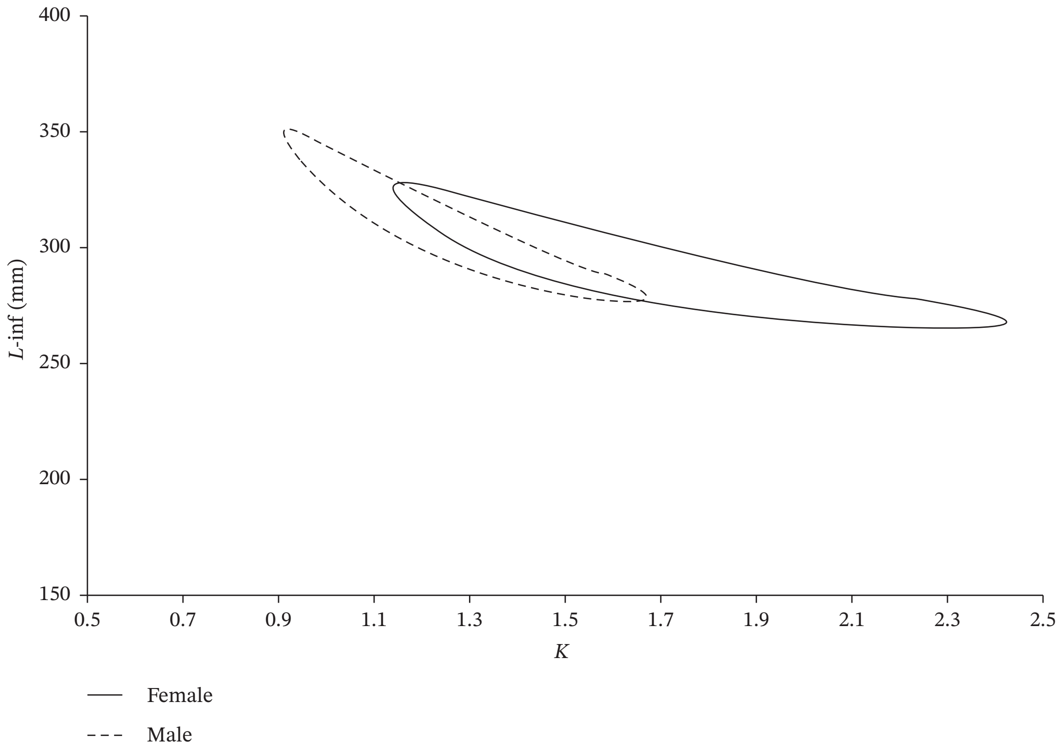

FIGURE 5 | Comparison of VBGF parameters for male and female *Siganus sutor*, depicting 95% confidence regions around least squares estimate of K and L_∞.

estimate by de Souza [18] (0.52 years^{-1}) and lower than the 0.88–0.93 years^{-1} reported by Wakeford et al. [30]. Collectively, these estimates suggest that annual mortality in *S. sutor* populations may range from approximately 52% to 93%, consistent with life-history strategies associated with rapid turnover and high productivity. When considered together, the demographic characteristics observed in this study—rapid growth, short longevity, high mortality and regular recruitment pulses—form a coherent life-history strategy consistent with the ecology of *S. sutor*. Such behavioural traits are typically associated with

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species that experience episodic but often strong recruitment and rely on rapid population turnover to sustain local abundance. In this context, the relatively high mortality rates estimated here likely reflect both natural predation pressures and fishing mortality in coastal artisanal fisheries. However, the species' extended spawning season and biannual recruitment pulses may partially buffer populations against high mortality by ensuring frequent replenishment of juvenile cohorts.

Overall, our results reinforce the view that *S. sutor* is a fast-growing, short-lived reef fish with high population turnover. These traits help explain the long-recognised productivity of *S. sutor* fisheries across the WIO, as rapid growth and frequent recruitment allow populations to replenish quickly. However, such life-history traits do not provide absolute immunity to population declines, particularly if persistent fishing pressure on spawning aggregations leads to recruitment variability. Robust demographic estimates, such as those presented here, therefore provide an essential foundation for improving stock assessments and developing management strategies capable of maintaining the resilience of this important coastal fishery. Future research should prioritise improved characterisation of early life-history stages, particularly juvenile growth rates, as well as the role of environmental and fishery drivers in shaping recruitment variability. Spatially explicit demographic studies across the species' distribution are also needed. It is plausible that *S. sutor* in the Indian Ocean comprises a set of semidiscrete subpopulations rather than a single panmictic metapopulation. Such population structuring, where subpopulations exhibit limited connectivity while retaining distinct characteristics (e.g., [32]), could help explain the wide variation in parameter estimates reported across regions and has important implications for fisheries assessment and management. Addressing these questions will be essential for developing adaptive, evidence-based management strategies capable of sustaining the productivity and resilience of *S. sutor* fisheries throughout the Indian Ocean.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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